BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)

José Francisco Bisbal Chinesta

Biogeografía e Impacto Humano en las comunidades de Anfibios y Reptiles del Cuaternario Final en la Península Ibérica: la Cueva de El Mirador (Atapuerca, Burgos) y la población de *Chalcides ocellatus* (Scincidae) de la Serra del Molar (Alicante)

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José Francisco Bisbal-Chinesta

TESIS DOCTORAL

Dirigida por

Dr. Hugues-Alexandre Blain

Tarragona, 2020

UNIVERSITAT ROVIRA i VIRGILI

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Portada: individuo adulto de *Vipera latastei* delante de la entrada de la Cueva del Mirador, Atapuerca. Autor: J.F. Bisbal-Chinesta.

Cover: adult individual of *Vipera latastei* in front of the entrance to the El Mirador cave, Atapuerca. Author: J.F. Bisbal-Chinesta.

Portada: individu adult de *Vipera latastei* davant de l'entrada de la Cueva del Mirador, Atapuerca. Autor: J.F. Bisbal-Chinesta.

A ma mare, Paqui i a mon pare, Pepe

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IPHES
Institut Català de Paleoecologia Humana i Evolució Social

HAGO CONSTAR que el presente trabajo, titulado "Biogeografía e impacto humano en las comunidades de anfibios y reptiles del Cuaternario final en la Península ibérica: la Cueva del Mirador (Atapuerca, Burgos) y la población de *Chalcides ocellatus* (Scincidae) de la Serra del Molar (Alicante)", que presenta José Francisco Bisbal-Chinesta para la obtención del titulo de Doctor, ha sido realizada bajo mi dirección en el Departamento de Historia e Historia del Arte de esta Universidad.

I DECLARE that the present work, entitled "Biogeography and human impact on the amphibian and reptile communities of the late Quaternary in the Iberian Peninsula: The El Mirador cave (Atapuerca, Burgos) and the population of *Chalcides ocellatus* (Scincidae) from the Serra del Molar (Alicante)", presented by José Francisco Bisbal-Chinesta to obtain the title of Doctor, has been carried out under my supervision in the Department of History and History of Art of this University.

Mayo 2020 / May 2020

Hugues-Alexandre Blain

Director de la Tesis Doctoral/ Director of the Doctoral dissertation

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Formato / Format

Esta tesis doctoral se presenta en un formato mixto de compendio de publicaciones y capítulos inéditos, que son futuras publicaciones. Para cumplir la normativa de la tesis por compendio de publicaciones, se han publicado tres trabajos en revistas incluidas en el *Journal Citation Report* (JCR). Las referencias de estos artículos publicados que también constituyen tres capítulos de la presente tesis son:

This doctoral thesis is presented in the mixed format of memory by compendium of publications and unpublished chapters, which are future publications. In order to comply with the requirements of the thesis by publication compendium, three papers have been published in international journals included in the *Journal Citation Report* (JCR). The references of these published papers that also constitute three chapters of the present thesis are:

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UNIVERSITAT ROVIRA I VIRGILI
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José Francisco Bisbal Chinesta

Índice de contenido / Index of contents

Índice de figuras / Index of figures

Índice de tablas / Index of tables

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
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Resumen

Esta tesis doctoral presenta la primera aproximación a la paleobiogeografía de los anfibios y reptiles de la Península Ibérica durante el Cuaternario final, basada en una síntesis comparativa del registro fósil conocido hasta ahora, desde el Musteriense hasta la Edad de Bronce. Por medio de Análisis de Correspondencia se han establecido dos grandes regiones bióticas durante el Pleistoceno tardío. La primera estaba localizada en el sur y centro de la Península Ibérica, con especies termófilas como las más representativas. La segunda región biótica estaba formada por la región atlántico-cantábrica y por el noreste ibérico, dominados por especies generalistas y eurosiberianas.

Después del Último Máximo Glacial se produjo la concurrencia en el norte de la Península ibérica de taxones autóctonos generalistas-eurosiberianos junto con especies termófilas, debido a una expansión de las especies mediterráneas meridionales. A partir del Holoceno, nuevas especies europeas penetraron en el norte, provenientes de otros refugios climáticos más orientales. La introducción de nuevas especies norteafricanas fue el último cambio paleobiogeográfico importante durante el Holoceno medio-tardío, posiblemente por el ser humano.

Con este marco general, la importancia del clima y de la influencia humana en la composición de las asociaciones de herpetofauna se analizan a través de dos casos de estudio. El primero son las egagrópilas de los niveles MIR4 y MIR5 de la Cueva de El Mirador (Sierra de Atapuerca, Burgos). Se trata de un conjunto de 20 acumulaciones de restos de pequeños vertebrados, contemporáneo al uso funerario de la cueva durante el Calcolítico y el Bronce inicial. El estudio taxonómico ha permitido identificar 350 individuos de 20 taxones diferentes, mayoritariamente herpetofauna. El análisis tafonómico de la acumulación con mayor número de restos, MIR5-P21-n4, ha corroborado su origen coprocenótico y ha postulado como agente acumulador un depredador de categoría 2, posiblemente una rapaz nocturna.

El análisis estadístico de las egagrópilas y de su contenido ha mostrado la existencia de diferencias cuantitativas y cualitativas en su composición faunística. Estas han sido interpretadas como variaciones estacionales entre el final del invierno y el verano, de acuerdo con la hibernación y con los ciclos reproductivos de los anfibios y reptiles. Según la reconstrucción paleoclimática, el clima era muy parecido al actual, aunque más lluvioso. La excepcional composición faunística de las egagrópilas se interpreta como un efecto secundario del impacto humano en el paisaje de la zona de Atapuerca, que habría obligado al depredador a cazar presas menos óptimas, pero más abundantes estacionalmente. La inclusión de las asociaciones de herpetofauna en el contexto septentrional ibérico del Holoceno las relaciona con la expansión posglacial de las especies termófilas.

El segundo caso de estudio es la nueva población de eslizón ocelado, *Chalcides ocellatus*, de la Serra del Molar (Alicante/Alacant), el primer registro de esta especie para la Península Ibérica. A través del estudio molecular de cinco individuos se ha determinado su origen filogeográfico en la zona oriental del Delta del Nilo. A partir de estos resultados, se ha postulado su translocación desde el Norte de Egipto a través del comercio marítimo entre el Levante mediterráneo y el sureste ibérico. El registro arqueológico regional muestra la llegada de productos comerciales y de grupos humanos provenientes de Egipto, especialmente durante la Edad del Hierro y la Edad Media, que incluso continúa actualmente a través de la importación de palmeras. Se plantea la hipótesis de la llegada de *C. ocellatus* como polizón entre la carga comercial y su posterior colonización de la Serra del Molar, donde habría sobrevivido gracias a las condiciones insulares de la zona hasta tiempos muy recientes.

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Abstract

This doctoral thesis presents the first approach to the Iberian palaeobiogeography of the different species of amphibians and reptiles from the Late Pleistocene (MIS 3) to present times, based on a comparative synthesis of the known fossil record, from the Mousterian to the Bronze Age. Correspondence Analysis has established two major biotic regions during the late Pleistocene. The first biotic region was in the center and south of the Iberian Peninsula, with thermophilic species as the most representative taxa. The second biotic region was formed by the Atlantic-Cantabrian facade and the northeast Iberian area, dominated by generalist and Euro-Siberian species.

Generalist-Eurosiberian and thermophilic species concur in the northern Iberian Peninsula after the Last Glacial Maximum, due to a northward expansion of southern Mediterranean species. Since the Holocene, newcomer European species entered through the northern Iberia, coming from other more eastern climatic refuges. The introduction of North African species was the last significant palaeobiogeographical change during the Middle-Late Holocene, possibly by humans.

Within this general framework, the importance of climate and human influence on the composition of herpetofauna associations is analysed in two case studies. The first is the pellets of the MIR4 and MIR5 levels from El Mirador cave (Sierra de Atapuerca, Burgos, northern Spain). This is a group of twenty accumulations of small vertebrate remains, contemporaneous with the burial use of the cave during the Chalcolithic and early Bronze Age. The taxonomic study has identified 350 individuals from 20 different taxa, mostly herpetofauna. Taphonomic analyses on the accumulation with the largest number of remains, MIR5-P21-n4, have corroborated its coprocenotic origin and have postulated a category 2 predator, possibly a nocturnal raptor, as the accumulating agent.

Statistical analysis on pellets and their contents has shown the existence of quantitative and qualitative differences in their faunistic compositions. These have been interpreted as seasonal variations between late winter and summer, in accordance with hibernation and the reproductive cycles of amphibians and reptiles. Based on the palaeoclimatic reconstruction, the climate was very similar to the current one, although rainier. The exceptional faunal composition of the pellets is interpreted as a secondary effect of the human impact on the landscape of the Atapuerca area, which would have forced the predator to hunt less optimal but seasonally more abundant prey. The inclusion of herpetofauna associations in the northern Iberian context of the Holocene relates them to the post-glacial expansion of thermophilic species.

The second case study is the new population of ocellated skink, *Chalcides ocellatus*, from the Serra del Molar (Alacant/Alicante, south-eastern Spain), its first record for the Iberian Peninsula. Their phylogeographic origin has been determined in the eastern zone of the Nile Delta, according to the molecular study of five individuals. Its translocation from Northern Egypt has been postulated via maritime trade between the Mediterranean Levant and the Iberian South-East. The regional archaeological record shows the arrival of commercial products and human groups from Egypt, particularly during the Iron Age and the Middle Ages, which even continues today with the importation of palm trees. The hypothesis of the arrival of *C. ocellatus* as a stowaway inside the commercial cargo and its later colonization of the Serra del Molar is proposed, where it has survived probably due to the insular conditions of the area until very recent times.

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Resum

Aquesta tesi doctoral presenta la primera aproximació a la paleobiogeografia dels amfibis i rèptils de la Península Ibèrica durant el Quaternari final, basada en una síntesi comparativa del registre fòssil conegut fins ara, des del Mosterià fins a l'Edat de Bronze. Per mitjà d'Anàlisis de Correspondència s'han establit dues grans regions biòtiques durant el Plistocè tardà. La primera estava localitzada en el sud i centre de la Península Ibèrica, amb espècies termòfiles com les més representatives. La segona regió biòtica estava formada per la regió atlàntico-cantàbrica i pel nord-est ibèric, dominades per espècies generalistes i eurosiberianes.

Després de l'Últim Màxim Glacial es va produir la concurrència en el nord de la Península ibèrica de tàxons autòctons generalistes-eurosiberians juntament amb espècies termòfiles, a causa d'una expansió de les espècies mediterrànies meridionals. A partir de l'Holocè, noves espècies europees van penetrar en el nord, provinents d'altres refugis climàtics més orientals. La introducció de noves espècies nord-africanes va ser l'últim canvi paleobiogeogràfic important durant l'Holocè mig-tardà, possiblement per l'ésser humà.

Amb aquest marc general, la importància del clima i de la influència humana en la composició de les associacions d'herpetofauna s'analitzen a través de dos casos d'estudi. El primer són les egagròpiles dels nivells MIR4 i MIR5 de la Cueva de El Mirador (Sierra de Atapuerca, Burgos). Es tracta d'un conjunt de 20 acumulacions de restes de xicotets vertebrats, contemporani a l'ús funerari de la cova durant el Calcolític i el Bronze inicial. L'estudi taxonòmic ha permés identificar 350 individus de 20 tàxons diferents, majoritàriament herpetofauna. L'anàlisi tafonòmic de l'acumulació amb major nombre de restes, MIR5-P21-n4, ha corroborat el seu origen coprocenòtic i ha postulat un depredador de categoria 2 com l'agent acumulador, possiblement una rapinyaire nocturna.

L'anàlisi estadística de les egagròpiles i del seu contingut ha mostrat l'existència de diferències quantitatives i qualitatives en la seua composició faunística. Aquestes han sigut interpretades com a variacions estacionals entre el final de l'hivern i l'estiu, d'acord amb la hibernació i amb els cicles reproductius dels amfibis i rèptils. Segons la reconstrucció paleoclimàtica, el clima era molt semblant a l'actual, encara que més plujós. L'excepcional composició faunística de les egagròpiles s'interpreta com un efecte secundari de l'impacte humà en el paisatge d'Atapuerca, que hauria obligat el depredador a caçar preses menys òptimes però més abundants estacionalment. La inclusió de les associacions d'herpetofauna en el context septentrional ibèric de l'Holocè les relaciona amb l'expansió posglacial de les espècies termòfiles.

El segon cas d'estudi és la nova població de lludrió ocel·lat, *Chalcides ocellatus*, de la Serra del Molar (Alacant), el primer registre d'aquesta espècie per a la Península Ibèrica. A través de l'estudi molecular de cinc individus s'ha determinat el seu origen filogeogràfic en la zona oriental del Delta del Nil. A partir d'aquests resultats, s'ha postulat la seua translocació des del Nord d'Egipte a través del comerç marítim entre el Llevant mediterrani i el sud-est ibèric. El registre arqueològic regional mostra l'arribada de productes comercials i de grups humans provinents d'Egipte, especialment durant l'Edat del Ferro i l'Edat mitjana, que fins i tot continua actualment a través de la importació de palmeres. Es planteja la hipòtesi de l'arribada de *C. ocellatus* com a polissó entre la càrrega comercial i la seua posterior colonització de la Serra del Molar, on hauria sobreviscut gràcies a les condicions insulars de la zona fins a temps molt recents.

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Résumé

Cette thèse doctorale présente la première approximation à la paléobiogéographie des amphibiens et des reptiles de la Péninsule Ibérique pendant le Quaternaire final, basée sur une synthèse comparative du registre fossile connu jusqu'au présent, depuis le Moustérien jusqu'à l'Âge du Bronze. Grâce à l'Analyse des Correspondances, deux grandes régions biotiques ont été mises en évidence au cours du Pléistocène supérieur. La première correspond au sud et au centre de la Péninsule Ibérique, étant les espèces thermophiles les plus représentatives. La seconde région biotique correspond à la partie atlantique et cantabrique et au nord-est ibérique, dominée par les espèces généralistes et eurosibériennes.

Après le Dernier Maximum Glaciaire, des associations se sont mise en place dans le nord de la Péninsule Ibérique comprenant des taxons autochtones généralistes-eurosibériens avec des espèces thermophiles, à cause d'une expansion des espèces méditerranéennes méridionales. À partir de l'Holocène, de nouvelles espèces européennes sont entrées par le nord, en provenance d'autres refuges climatiques plus orientaux. L'introduction de nouvelles espèces nord-africaines a été le dernier changement paléobiogéographique important au cours de l'Holocène moyen-tardif, probablement causé par l'homme.

Dans ce cadre général, l'importance du climat et de l'influence humaine dans la composition des associations d'herpétofaune sont analysées selon deux cas d'études. Le premier cas se basera sur une étude de pelotes de réjection provenant des niveaux MIR4 et MIR5 de la Cueva de El Mirador (Sierra de Atapuerca, Burgos, Nord de l'Espagne). Il s'agit d'un ensemble de 20 accumulations de restes de petits vertébrés, contemporaine à l'usage funéraire de la grotte au cours du Chalcolithique et du début de l'Âge du Bronze. L'étude taxonomique nous a permis d'identifier 350 individus de 20 taxons différents, principalement des amphibiens et des reptiles. L'analyse taphonomique de l'accumulation possédant le plus grand nombre de restes, MIR5-P21-n4, a corroboré son origine coprocénotique et a permis de proposer un prédateur de catégorie 2, probablement un rapace nocturne, comme agent accumulateur.

L'analyse statistique des pelotes de réjection et de leur contenu a montré l'existence de différences quantitatives et qualitatives concernant leur composition faunistique. Celles-ci ont été interprétées comme des variations saisonnières entre la fin de l'hiver et l'été, en accord avec l'hibernation et les cycles de reproduction des amphibiens et des reptiles. Selon la reconstruction paléoclimatique, le climat était très similaire à l'actuel, bien que plus pluvieux. La composition faunistique exceptionnelle de ces pelotes de réjection est interprétée comme un effet secondaire de l'impact humain sur le paysage de la région d'Atapuerca, ce qui aurait forcé le prédateur à consommer des proies moins optimales mais plus abondantes pendant la saison concernée. L'inclusion des associations herpétofauniques à l'intérieur du contexte septentrional ibérique de l'Holocène les associent avec l'expansion postglaciaire des espèces thermophiles.

Le deuxième cas d'étude est la nouvelle population des scinques ocellés, *Chalcides ocellatus*, de la Serra del Molar (Alacant, Sud-Est de l'Espagne), qui représente la première mention pour cette espèce dans la Péninsule Ibérique. Grâce à l'étude moléculaire de cinq individus, l'origine phylogéographique de cette population a été déterminée comme provenant de la parte orientale du Delta du Nil. Sur la base de ces résultats, nous proposons leur translocation depuis le nord de l'Egypte à travers du commerce maritime entre la Méditerranée orientale et le sud-est ibérique. Les données archéologiques régionales montrent l'arrivée de produits commerciaux et de groupes humains d'Egypte, spécialement pendant l'Âge du Fer et le Moyen Âge, et qui continue aujourd'hui avec l'importation de palmiers. Nous proposons comme hypothèse une arrivée de *C. ocellatus* voyageant comme passager clandestin au milieu de la cargaison commerciale, lui ayant permis sa colonisation ultérieure de la Serra del Molar, où il aurait survécu grâce aux conditions insulaires de la zone jusqu'à des temps très récents.

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Chapter 1

Introduction. Long-term changes in composition and distribution patterns in the Iberian herpetofaunal communities since the latest Pleistocene

Abstract

The climate has undergone significant changes since the end of the Last Glacial Maximum and in the course of the Holocene, parallel to important cultural transformations and migrations in the human communities. The faunal record has also suffered the effects of climate change. Amphibians and reptiles in particular have been shown to be highly sensitive because they are very susceptible to temperature alterations due to their ectothermy. This research presents the first approach to the Iberian palaeobiogeography of the different species of amphibians and reptiles from the Late Pleistocene (MIS 3) to present times, based on a comparative synthesis of the latest research published in recent years and the fossil record of the 58 archaeo-palaeontological sites with significant assemblages. The palaeoherpetofaunal associations make it possible to establish two major biotic regions during the Late Pleistocene. The first biotic region was located in the center and south of the Iberian Peninsula, with thermophilic species as the most representative taxa. The second biotic region was formed by the Atlantic-Cantabrian facade and the northeast Iberian area, dominated by generalist and Euro-Siberian species, with an absence of Mediterranean species. After the Last Glacial Maximum there was an unprecedented concurrence in the northern Iberian Peninsula of autochthonous taxa from that area with thermophilic species, due to a northward expansion of Mediterranean species. In the early Holocene, new species with no previous record in the Iberian Peninsula entered northern Iberia from eastern Mediterranean *refugia*. Finally, the introduction of North African species was the last significant biogeographical change during the Middle-Late Holocene.

1.1. Introduction

The last 60,000 years of the Quaternary have been characterized in Western Europe by major climatic and environmental changes as a result of the occurrence of the last great glacial pulsation and the beginning of the current warm interglacial. This time interval begins in MIS 3 (ca. 60,000 to 26,900 BP), alternating between phases of warming and cooling climate that correspond to the decline or increase of forests and semi-desert environments until the onset of MIS 2 (26,900 to 14,900 BP). At this point there occurs a major cooling process and a remarkable expansion of open arid spaces, with vegetation typical of cold and dry environments and with forest limited to areas of refuge (Fletcher and Goñi, 2008; Fletcher et al., 2010). MIS 1 (which starts at 14,900 BP) is characterized by a generalized warming of the climate, especially from the Holocene onwards (11,700 BP), and by a rapid increase in wooded areas. However, this phase also

presents significant climatic fluctuations, though without outweighing the warm overall dynamic (Fletcher and Goñi, 2008; Fletcher et al., 2009; Walker et al., 2012; Naughton et al., 2015).

These large climatic and environmental changes have had a decisive impact on wildlife. The herpetofauna, reptiles and amphibians, is one of the animal groups that is most sensitive to temperature fluctuations due to the characteristic ectothermy of such organisms (Pough, 1980). This makes it a group of special interest for studying the effects that Quaternary climate changes have had on biodiversity (Araújo et al., 2008). All species of reptiles and amphibians in the Iberian fossil record of the Late Quaternary are currently represented in the Iberian Peninsula (Rage and Roček, 2002; Blain et al., 2011, 2014a, 2016). This facilitates actualist studies that allow us to observe the movements that have occurred in the geographical distribution of these groups leading to the current situation and to infer the possible palaeoenvironmental and bioclimatic changes at a regional level (Blain, 2009).

To date, 51 species of reptiles and 28 species of amphibians have been described on the Iberian mainland, a herpetofaunal assemblage characterized by a great variability of thermal and ecological requirements (Masó and Pijoan, 2011). This includes typically Mediterranean taxa such as *Acanthodactylus erythrurus*, *Hemidactylus turcicus*, *Hemorrhois hippocrepis*, *Chamaeleo chamaeleon* and *Blanus cinereus*, and other species associated with Euro-Siberian climates such as *Lacerta agilis*, *Zootoca vivipara*, *Mesotriton* (*Ichthyosaura*) *alpestris* and *Rana temporaria*. The widespread mountainous terrain of the Iberian Peninsula has facilitated the emergence of species whose distribution is associated with high mountain climates, especially in northern Spain, examples being *Calotriton asper* and the genus *Iberolacerta* (Carretero et al., 2018). The high degree of knowledge currently available of the 79 herpeto-faunal species with a current distribution in the Iberian Peninsula (Pleguezuelos et al., 2002; Masó and Pijoan, 2011; Salvador and Pleguezuelos, 2013; Carretero et al., 2018) results in a good bibliographical, biogeographical and statistical base for an analysis of the Iberian fossil herpetofauna. The biological requirements of each of these species generate particular restrictions that limit their biogeographical distribution and the viability of their populations, both at present and during the Quaternary, allowing us to infer the palaeoclimate and the palaeobio-geography by means of the fossil record (Blain et al., 2009a).

The phylogenies of different European species suggest the existence of a climatic refuge in the Iberian Peninsula through the successive glacial stages, from which these species would have subsequently repopulated the rest of the continent during the interglacial phases. This is a role similar to that played by the other peninsulas of southern Europe, the Balkans and Italy (Hewitt, 1996, 2000), made possible by the special climatic characteristics of their geographical location (Fletcher et al., 2010; Harrison and Sánchez-Goñi, 2010). In addition, the highly variable Iberian orography allowed the existence of a multitude of areas with different climatic and environmental characteristics, permit-ting the survival of species more adapted to temperate climates, in contrast to the

situation in the rest of the continent (Nieto, 2011).

In the present study, by means of a comparative statistical analysis of the herpetofaunal associations from a total of 118 levels of 38 Iberian archaeo-palaeontological sites in the Iberian Peninsula from the last 60,000 years (Figure 1.1), we intend to identify the main changes in the distribution, composition and diversity of the reptiles and amphibians during the time interval analyzed. Our aim is to determine the main biogeographical movements of the different herpetofaunal species throughout the Iberian Peninsula and the role of the peninsula as a climate refuge during the Last Glacial Maximum and as a starting point for the subsequent re-colonization of northern areas.

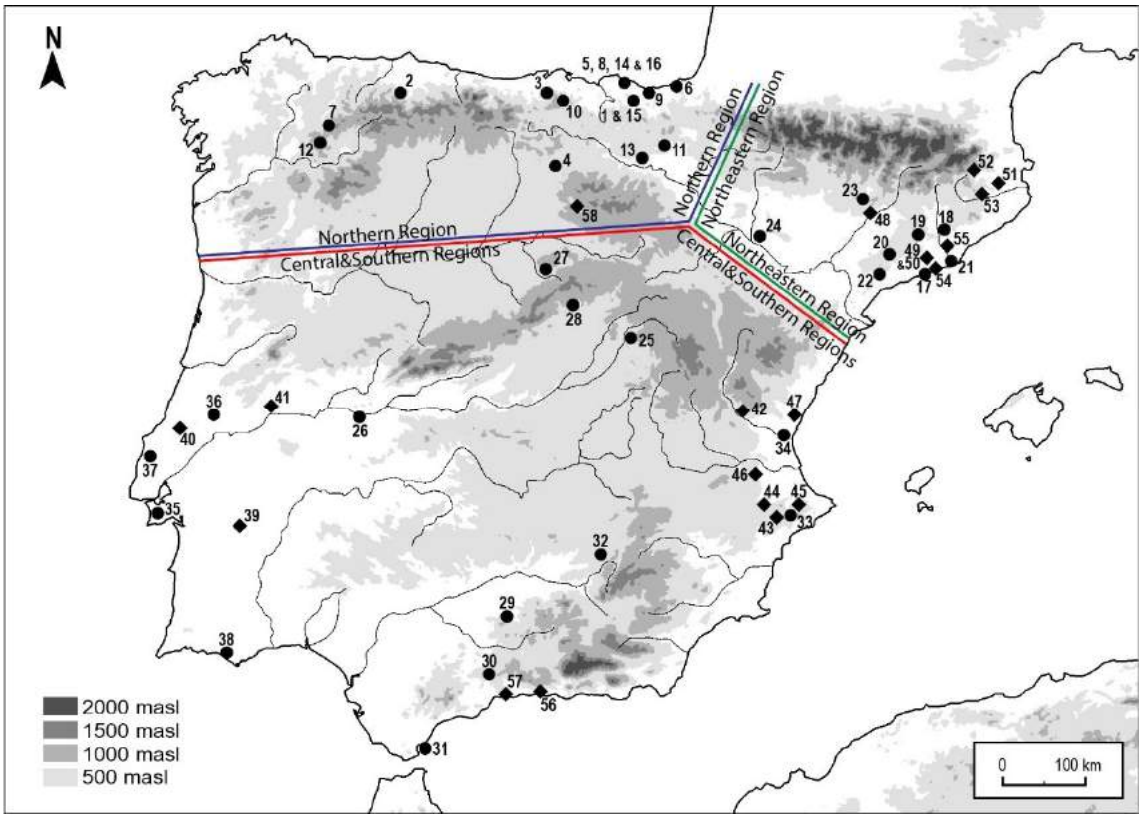

Figure 1.1.- Map with the latest Pleistocene-Late Holocene archaeo-palaeontological sites with herpetofaunal assemblages includes in the data matrices: **1)** Askondo, **2)** Cueva del Conde, **3)** Cueva de Cobrante, **4)** El Portalón, **5)** Santimamiñe, **6)** Erralla, **7)** Valdavara-1, **8)** Laminak II, **9)** Aizkoltzo, **10)** El Mirón, **11)** Las Orcillas-1, **12)** Cova Eirós, **13)** Peña Larga, **14)** Antoliñako Koba, **15)** Dolmen of Errekatxuetako Atxa, **16)** Santa Catalina, **17)** Cova del Gegant, **18)** Cova Teixoneres, **19)** Abric Romaní, **20)** Cova dels Xaragalls, **21)** Riera de Canyars, **22)** Cova dels Galls Carboners, **23)** Cova Colomera, **24)** Balsa la Tamariz, **25)** Cueva de los Torrejones, **26)** Sala de las Chimeneas of Maltravieso, **27)** Peña de Estebanvela, **28)** Ventana, **29)** Sima de Abraham, **30)** Boquete de Zafarraya, **31)** Gorham's Cave, **32)** Castillejo del Bonete, **33)** Abric del Salt, **34)** Lloma de Betxí, **35)** Gruta da Figueira Brava, **36)** Gruta do Caldeirão, **37)** Gruta Nova da Columbeira, **38)** Guia of Albufeira, **39)** Gruta do Escoural, **40)** Gruta da Oliveira, **41)** Foz do Enxarrique, **42)** Abrigo de la Quebrada, **43)** Abric del Pastor, **44)** Cova Canet, **45)** Cova de l'Or, **46)** Ereta de Pedregal, **47)** Pic dels Corbs, **48)** Roca dels Bous, **49)** Cova del Toixò, **50)** Can Sadurní, **51)** La Draga, **52)** Pont de Sadernes, **53)** El Pasteral, **54)** Cal Tintorer, **55)** Bòbila Madurell, **56)** Cueva de Nerja, **57)** Cueva de Rincón de la Victoria, and **58)** Cueva Millán. The sites marked with a circle are those included in the regional data matrices, while those marked with a rhombus have been excluded from them.

1.2. Material and Methods

1.2.1. *Data matrix*

First, a bibliographical search has been carried out in the major journals of archaeology, palaeontology and zooarchaeology, as well as a search through the major Internet search engines (mainly Google, Yahoo and Bing) and academic websites (Universities, Researchgate, Academia.edu, Google Scholar). For our statistical studies, the taxa identified in 118 levels of 38 palaeo-archaeological sites chronologically dated to between early MIS 3 (*ca*. 60,000 BP) and the Bronze Age (*ca*. 3,500 BP) have been compiled. These were then separated into three data matrices on the basis of biogeographical factors (Appendices 1, 2 and 3). For each level all the species present in the herpetological record have been included. In the case of genera with a single Iberian species (e.g., genus *Pelobates*), either currently or in the Quaternary fossil record (genus *Testudo*) (Morales and Sanchis, 2009), these have been assigned to the only species in question. The same goes for taxonomic identifications assigned to families that only have a single species present in the Iberian Peninsula (Geoemydidae or Emydidae). However, we have not included the genus-level citations of genera that have two or more species present in the Iberian Peninsula (e.g., genera *Bufo* sensu lato and *Natrix*).

In addition, we have applied some corrections to the data matrix to reduce dispersion and facilitate interpretation. The genus-level citations of the genera *Hyla*, *Lacerta* and *Vipera* from levels in the northern area have been included because of their biogeographical significance. For the same reason, the genus-level citations of *Pelodytes* and *Alytes* have also been included, despite the lack of species-level identification in some cases (e.g., Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013; Blain et al., 2013). Due to the problems in the palaeontological literature of differentiating between *R. temporaria* and *Rana iberica* by osteological criteria (e.g., Zubeldia et al., 2007; Murelaga et al., 2011; García-Ibaibarriaga et al., 2015), these two species have been grouped together as *R. temporaria-iberica* in the data matrix of the northern region. The citations of *Elaphe* sp., a snake genus that previously grouped together the current species *Zamenis scalaris* and *Zamenis longissimus*, have been assigned to *Z. scalaris* in the cases from Las Orcillas 1 and Lloma de Betxí, in accordance with the Iberian thermophilic tendencies of the herpetofaunal associations from their respective levels (Fernández et al., 2010; Tormo and de Pedro, 2013).

There are 20 levels with herpetofaunal record that have not been included in the matrix data. The chelonian citations from the palaeo-archaeological sites of Gruta da Oliveira, Foz do Enxarrique, Abrigo de la Quebrada, Abric del Pastor, Cueva de San Luís, Cova Canet, Gruta do Escoural, Cova de l'Or, Ereta del Pedregal, Pic dels Corbs, Roca dels Bous, Cova del Gegant, Cova del Teixò, Can Sadurní, La Draga, Pont de Sadernes, El Pasteral, Cal Tintorer and Bòbila Madurell, as well as levels NV13, NM14 and NM4-2 of Cueva de Nerja (Jiménez Fuentes, 1986; Fernández Peris and Martínez Valle, 1989; Pérez Ripoll, 1990; Jiménez-Fuentes et al., 1998; Gómez and Jiménez Fuentes, 1998; Brugal and Raposo, 1999; Crespo, 2002; Mora et al., 2003; Budó et al., 2005; Fèlix et al., 2006; Morales and Sanchis 2009; Aura et al., 2010; Jordá et al., 2011;

Daura and Sanz, 2012; Sanchis et al., 2013, 2015; Pérez Ripoll, com. pers.), the citation of *Tarentola mauritanica* from level A.sup of Cova Colomera (López-García et al., 2010a), the citation of *R. iberica* from Cueva Millán (Esteban and Sanchiz, 1990) and the citation of *C. chamaeleon* from Cueva de Rincón de la Victoria (Talavera and Sanchiz, 1983) have been excluded from the northeastern and central-southern data matrices, to avoid statistical deviations owing to the large number of mono-specific citations without any other herpetofaunal taxa, although they are included in the subsequent discussion. Also, the citations of the genus *Testudo* that date from the Holocene of the northeastern area (Budó et al., 2005) have not been included because of the taxonomic revision they have undergone (Fèlix et al., 2006; Morales and Sanchis, 2009).

In order to compare the fossil record with the current situation, we have collected data on the present-day herpetofaunal assemblages from the same 10x10 km UTMs as the archaeo-palaeontological sites included in the regional data matrices, through the "*Especies por UTM*" (species per UTM) function of the SIARE application website (*Sistema de Información de Anfibios y Reptiles de España*) (AHE, 2016-2020).

1.2.2. *Classification of levels*

The 118 levels have been grouped, in accordance with the geographical situation of the 38 different palaeo-archaeological sites (Figure 1.1; Table 1.1), into three data matrices (Appendices 1, 2 and 3). In each data matrix, species with a regional fossil record have been grouped into the rows, while the archaeo-palaeontological levels, with their corresponding taxonomic lists, have been grouped into the columns. Therefore, in the binary data base the presence of a taxon is marked by "1" and its absence by "0". The three resultant data matrices are:

· Northern Region: this includes 16 sites located between Galicia and Navarra, covering the entire Cantabrian fringe and inner area as far as Portalón de Atapuerca at its southern boundary. This region is currently characterized by a humid climate due to the Atlantic influence, with rather cold winters and temperate summers. Overall, there is a good distribution of levels throughout the studied period and all the archaeological cultures known for this region are represented: the Mousterian associated with *Homo neanderthalensis* and the Aurignacian, Gravettian, Solutrean, Magdalenian, Azilian, Microlaminar Epipaleolithic, Mesolithic, Neolithic, Chalcolithic, Bell Beaker and Bronze Age that are linked to Anatomically Modern Man. A total of 75 archaeo-palaeontological levels (Table 1.1) and 24 different taxa have been included in the data matrix for the northern region (Appendix 1).

· Northeastern Region: this includes 8 sites located in present-day Catalonia and Aragon, from the Mediterranean to the Pyrenees and the Middle Ebro Valley, in the northern area of the Mediterranean side of Iberia. Most of these sites are dated to MIS 3 while most of the MIS 1 records are mono-specific chelonian citations, which

Sites	Levels	Region	References
1. Askondo	13, 9, 8, 7, 6, 5, 3, 2 & 1	North	Garete & Rios-Garaizar, 2011; García-Ibaibarriaga et al., 2015
2. Cueva del Conde	N104, N103, N10b, N20a, N2a1 & N2a2	North	Arbizu et al., 2005; López-García et al., 2011c
3. Cobrante	N7 to N1	North	Rasines, 2009; Martín et al., 2009
4. El Portalón	P16 to P1	North	Carretero et al., 2008; Ruiz-Zapata et al., 2008; López-García et al., 2010b
5. Cova Eirós	3 & 2	North	Rey-Rodríguez et al., 2016
6. Antoliñako Koba	D, C, B & A	North	Zubeldia et al., 2007
7. Santimamiñe	Arg-o, Camr, Csn, Balm, Almp, Slnc, Arcp, Slm & Lsm	North	Murelaga et al., 2011; Rofes et al., 2014
8. Erralla	VI, V, IV, III & II	North	Esteban & Sanchiz 1985; Peman 1985; Altuna 1985
9. Valdavara-1	Lower & Upper Units	North	Vaquero et al., 2009; Blain et al., 2009b; López-García et al., 2011b
10. Santa Catalina	III, II & I	North	Arribas & Berganza, 2010; Bailon & García-Ibaibarriaga, 2014
11. Laminak II	II-I	North	Arribas & Berganza, 1989; Sanchiz & Esteban 1994; Peman, 1994; Berganza & Arribas, 1994
12. Aizkoltzo	L.15-12	North	Murelaga et al., 2008
13. El Mirón	10 to 3	North	Straus et al., 2001; Sanchiz et al., 2012
14. Las Orcillas-1	C.II-I	North	Fernández et al., 2010
15. Peña Larga	IV-I	North	Castaños 1997; Murelaga et al., 2009; Rofes et al., 2013
16. Errekatxuetako Atxa's Dolmen	Bell Beaker level	North	Murelaga et al., 2007
17. Teixoneres	IIb & II	North-East	Tissoux et al., 2006; Rosell et al., 2010, 2014; López-García et al., 2012b, 2014a
18. Cova del Gegant	V, IV & III	North-East	Daura et al., 2005, 2010; Daura & Sanz, 2012; López-García et al., 2007, 2008, 2012a, 2014a
19. Abric Romaní	O, K, J, E & D	North-East	Burjachs & Julià, 1994; Burjachs et al., 2012; López-García et al., 2014a
20. Xaragalls	C8 to C3	North-East	López-García et al., 2012c
21. Terrassa de la Riera dels Canyars	Fluvial deposit	North-East	Daura et al., 2013; López-García et al., 2013, 2014a
22. Galls Carboners	L.108-105	North-East	López-García et al., 2014b
23. Cova Colomera	C15, C14-15, C12 & EE1	North-East	Oms et al., 2009; López-García et al., 2010a
24. Balsa la Tamariz	Burial sites and prehistoric settlement	North-East	Royo & Rey, 1993; Rey & Royo, 1993; Laplana & Cuenca-Bescós, 1995
25. Cueva de los Torrejones	L.5-4	Center & South	Arribas et al., 1995, 1997
26. Sala Chimeneas, Maltravieso	A	Center & South	Rodríguez et al., 2009; Bañuls-Cardona et al., 2012
27. Peña de Estebanvela	VI, IV, III, II & I	Center & South	Sanchiz & Barbadillo, 2007; Sanchiz & Bailon, 2013; Cacho et al., 2013
28. Cueva de la Ventana	Units 7-9-16-22-26, 14-18-26 & 3-4	Center & South	Sánchez Marco et al., 2005
29. Sima de Abraham	Deposit 11	Center & South	Martínez-Sánchez et al., 2010, 2012
30. Boquete de Zafarraya	Unit Id-Ia	Center & South	Barroso & Bailon, 2003; Barroso et al., 2003; Zilhao, 2006
31. Gorham's Cave	IV, IIIb & IIIa	Center & South	Gleed-Owen, 2001; Finlayson et al., 2006; Jennings et al., 2011; López-García et al., 2011a; Blain et al., 2013
32. Castillejo del Bonete	Sedimentary filling of the burial tumulus	Center & South	Benítez de Lugo et al., 2015
33. Cova del Salt	XI	Center & South	Pérez Luís, 2014
34. Lloma de Betxí	Bronze Age settlement	Center & South	De Pedro, 2009; Tormo & De Pedro, 2013
35. Gruta da Figueira Brava	Mousterian sequence	Center & South	Crespo et al., 2000; Lapparent de Broin & Antunes, 2000; Crespo, 2002
36. Gruta do Caldeirão	Mousterian sequence	Center & South	Crespo, 2002
37. Gruta Nova da Columbeira	Mousterian sequence	Center & South	Jiménez Fuentes et al., 1998; Crespo, 2002
38. Guia de Albufeira	Postglacial Pleistocene sequence	Center & South	Crespo, 2002

Table 1.1.- List of the latest Pleistocene-Late Holocene archaeo-palaeontological sites and levels included in the regional data matrices.

have not been included in the data matrix. At present, there are no sites in this area with published herpetofauna dated to MIS 2. The human cultures represented in the total of 23 archaeological levels (Table 1.1) are Mousterian, Neolithic and Bronze Age and 17 different herpetofaunal taxa have been included in the data matrix for the northeastern zone (Appendix 2).

· Central and Southern Regions: this group includes 14 sites in the Mediterranean area, mainly distributed in Castilian and Extremaduran areas, Andalusia, central and southern Portugal, and the center of the Valencia Country. The human cultures represented in the 22 archaeological levels (Table 1.1) are the Mousterian, Solutrean, Magdalenian, Epipaleolithic, Neolithic, the Motillas Culture and the Valencian Bronze Culture. In the data matrix for these areas 29 different taxa have been included (Appendix 3).

1.2.3. *Statistical methodology*

The method of hierarchical clustering has been chosen to perform the statistical analysis, because this generates a dendrogram that reveals the relationships of similarity and difference between the species concurring in the archaeo-palaeontological levels included in the data matrices. The aim is to infer whether or not the resulting herpetofaunal groups are based on chronostratigraphic criteria whose origins are related to possible biogeographic changes. In addition, the Jaccard similarity index has been applied, since this is recommended for clustering binary data, because it gives more importance to joint occurrences in the assemblages (Hammer et al., 2001). Also, the "unweighted pair-group average" has been applied to the three data matrices, resulting in the union in the dendrogram of different groups based on the average distance between their members.

Moreover, a Correspondence Analysis (CA) has been used to support the results of the hierarchical clustering. The CA is the recommended method for comparing associations (assigned to columns) with the total count of taxa, or identifying taxa (assigned to rows) through the associations (Greenacre, 2010). In the case of this paper its aim is to mark the relationships of proximity between taxa of different associations, grouping them closely in contrast to the more atypical taxa, which will appear in an eccentric position in relation to the rest of the set. The *Paleontological Statistics* program (PAST3) has been used for all statistical approaches (Hammer et al., 2001).

1.3. Results

A preliminary analysis of the data matrices shows clear differences in the typical composition of the three analyzed areas. For the prehistoric sequence of the northern region the most representative species are *R. temporaria* (or *R. temporaria-iberica*) (present in 69 assemblages, 90.8% of the total), *Anguis fragilis* (35 assemblages, 46.1%), *Bufo* gr. *Bufo bufo* (*Bufo spinosus* in current Iberian regions) (32 assemblages, 42.1%) and to a lesser extent *Epidalea calamita* (29 assemblages, 38.1%), the genus *Alytes* (27 assemblages, 35.5%) and the genus *Vipera* (19 assemblages, 25%) (Appendix

1), forming a typical association of forest environments and wet meadows. For the northeastern Iberian area the most significant taxa are *E. calamita* (13 assemblages, 56.5%), *R. temporaria* (12 assemblages, 52.2%), *Alytes obstetricans* (11 assemblages, 47.8%) and *A. fragilis* (10 assemblages, 43.5 %) and to a lesser extent *Bufo* gr. *B. bufo* (9 assemblages, 39.1%), *Coronella girondica* (8 assemblages, 34.8%) and *Pelodytes punctatus* (8 assemblages, 34.78%) (Appendix 2), which form a herpetofaunal association with a marked preference for humid environments and high rainfall, with the exception of *C. girondica*. Both zones located in the northern third of the Iberian Peninsula share a herpetofauna with hygrophilous tendencies and a predilection for humid environments. However, the prevalence of *E. calamita* at the expense of *R. temporaria* in the northeastern region, coupled with the significant presence of *P. punctatus* and *C. girondica*, can be related to the greater influence of Mediterranean environments, correlated with its geographical position in the Western Mediterranean basin.

In contrast, a Mediterranean influence and thermophilic tendencies become more evident in the herpetofaunal fossil record of the remaining two thirds of the Iberian Peninsula, comprising the central, eastern and southern areas. In these regions the predominant species are *E. calamita* (15 assemblages, 68.2%), *Timon lepidus* (14 assemblages, 63.6%), *Bufo* gr. *B. bufo* (11 assemblages, 50%), *Z. scalaris* (10 assemblages, 45.4%) and in lesser measure *Pelobates cultripes* (8 assemblages, 36.4%), *Testudo hermanni* (8 assemblages, 36.4%), *Malpolon monspessulanus* (7 assemblages, 31.8%), *Pleurodeles waltl* (6 assemblages, 27.3%) and *Vipera latastei* (6 assemblages, 27.3%) (Appendix 3). Together, these species are a typical association in current Mediterranean dry environments with a water regime that is markedly seasonal and the presence of open environments, scrubs and forests.

Application of the statistical analysis methods CA and hierarchical clustering to the three data matrices shows remarkable and consistent trends between the two methods. In the northern region the resulting cluster distinguishes three groups (Figure 1.2.A). The first group is formed by the species *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria-iberica*, *A. fragilis* and the genera *Alytes* and *Vipera*, an association of generalist herpetofauna that is tolerant to Euro-Siberian conditions. In addition, these taxa are the only ones present in the fossil record of the Cantabrian fringe during MIS 2, the last glacial phase, and they are almost exclusive during MIS 3.

The second cluster group is composed of the species *Coronella austriaca*, *Natrix maura*, *Chalcides striatus*, *I. alpestris*, *C. girondica*, *Hierophis viridiflavus*, *Lissotriton helveticus*, *Natrix natrix*, *Z. longissimus*, *Salamandra salamandra* and the genera *Hyla* and *Lacerta*. With the exception of *S. salamandra*, which has a fossil record from Cueva del Conde in MIS 3 (López-García et al., 2011c), all are hygrophilous and/or generalist taxa, tolerant to a Euro-Siberian influence, which appear in the regional fossil record during MIS 1, i.e. during the last postglacial and interglacial stages.

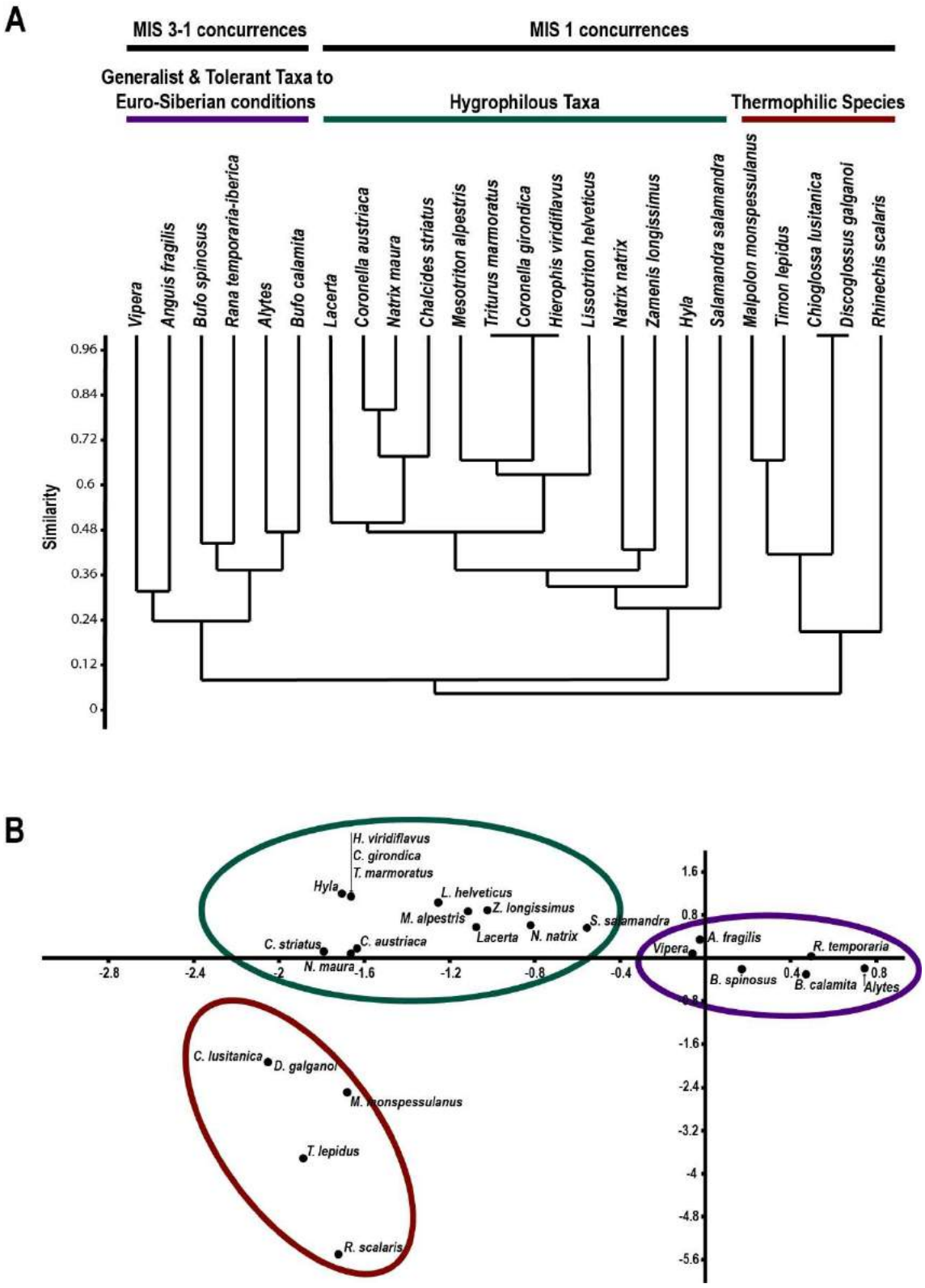

Figure 1.2.- Northern Iberian herpetofaunal record: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the Correspondence Analysis of latest Pleistocene-Late Holocene assemblages.

Finally, the third group in the regional cluster is formed by *Chioglossa lusitanica*, *Discoglossus galganoi*, *T. lepidus*, *Z. scalaris* and *M. monspessulanus*. These five species also appear in the fossil record of the Iberian North during MIS 1. Except for *C. lusitanica*, which is a salamander endemic to the northwestern Iberian region (Vences, 2002), the remaining taxa are thermophilic species linked to the Mediterranean influence. This is due to the presence of the unique fossil record of *C. lusitanica* in the herpetofaunal assemblage of the Upper Unit of Valdavara-1, where also appears another thermophilic herpetofauna as *D.* cf. *galganoi*, *T. lepidus* and *M. monspessulanus* (Blain et al., 2009b; López-García et al., 2011a).

The same overview is obtained by CA, the same three groups appearing in the graphical representation of CA (Figure 1.2.B). The species present in the northern assemblages in MIS 3 and MIS 2 have been grouped in the right half of the graph. *S. salamandra*, absent in MIS 2 but present in MIS 3, appears in the graph in a slightly eccentric position relative to the rest of the group of hygrophilous and/or generalist species of MIS 1, but it is not grouped together with the taxa of the glacial phase, which are located in the right third of the graph.

For the northeastern Iberian region the same scenario as in the northern zone is partially repeated, although the lack of a herpetofaunal record for MIS 2 rules out any further comparison between these two Iberian regions. In the northeastern cluster the tripartite scheme is repeated (Figure 1.3.A). The first group is formed by *P. cultripes*, *T. lepidus*, *Z. scalaris* and *M. monspessulanus*, thermophilic species of Mediterranean influence that appear in the regional record in MIS 1, even though *P. cultripes* has a previous record in MIS 3 (López-García et al., 2012a).

The second group is formed by the species that occur in the fossil record of this region for MIS 3: *S. salamandra*, *A. obstetricans*, *P. punctatus*, *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria*, *A. fragilis*, *C. austriaca*, *C. girondica*, *Vipera aspis* and *V. latastei*.

The third group is composed of *N. maura* and *C. asper*, which appear in the regional record in MIS 1. *N. maura* is a water snake with generalist trends, while *C. asper* is a newt endemic to the Pyrenees Mountains. Applying CA to the same data matrix shows a clear separation of thermophilic Mediterranean species with respect to the other taxa. It also shows a position near the binomial *C. asper* and *N. maura* for the conjunction of species from MIS 3, though separated from them, in correlation with the hygrophilous, tolerant tendencies of both groups (Figure 1.3.B).

Finally, for the central-southern quadrants of the Iberian Peninsula, the dendrogram is much less clear compared to the previous two. In this case the different groups do not correspond to chronological criteria, suggesting possible stability in the composition of the herpetofaunal fossil record of this region, which is entirely composed of typical Iberian Mediterranean species (Figure 1.4.A). However, the existence of potential biases in the fossil record and / or data matrix cannot be ruled out. These could be indicated in the cluster by the position of the three chelonian species,

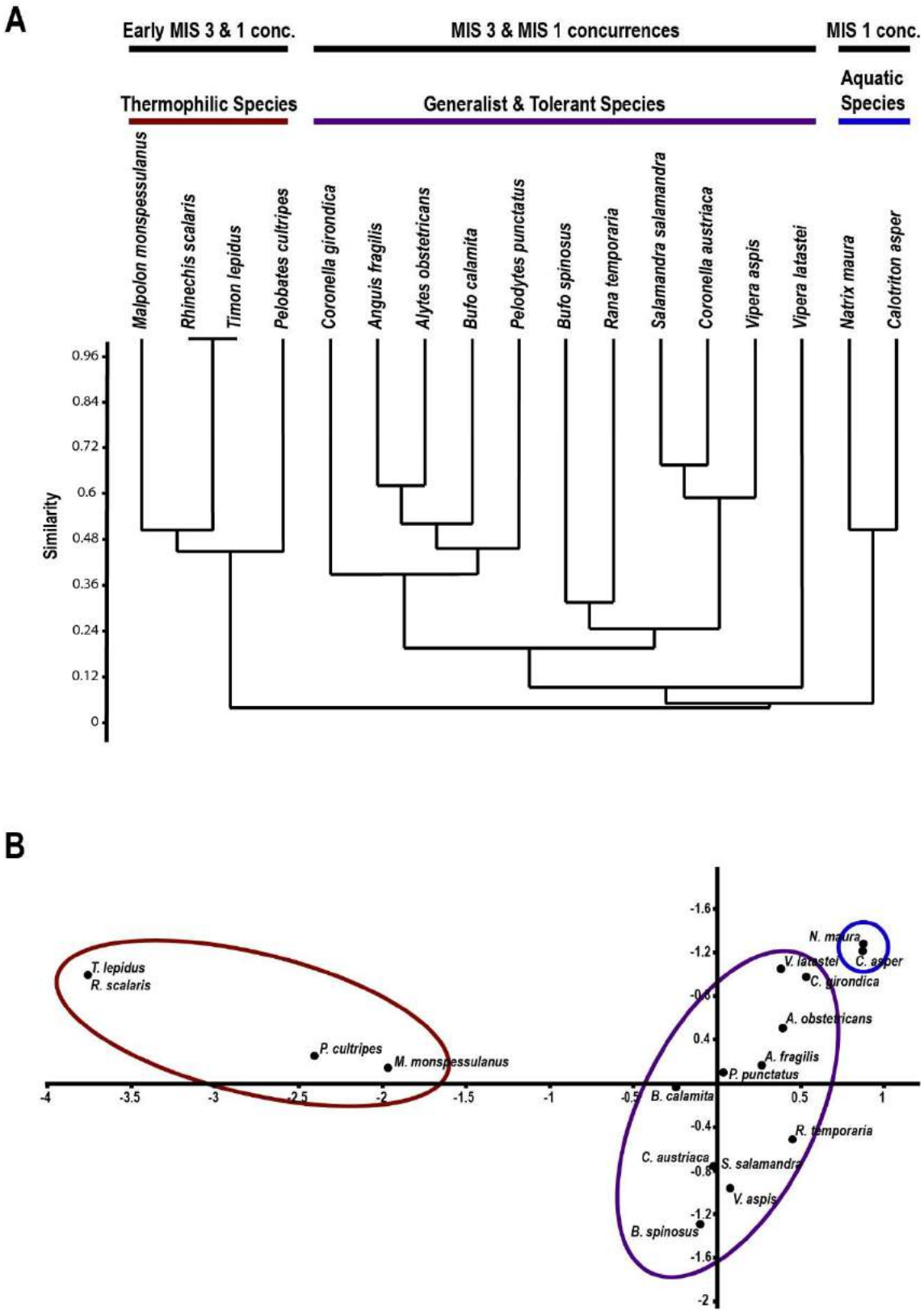

Figure 1.3.- Northeastern Iberian herpetofaunal record: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the Correspondence Analysis (C) of latest Pleistocene-Late Holocene assemblages.

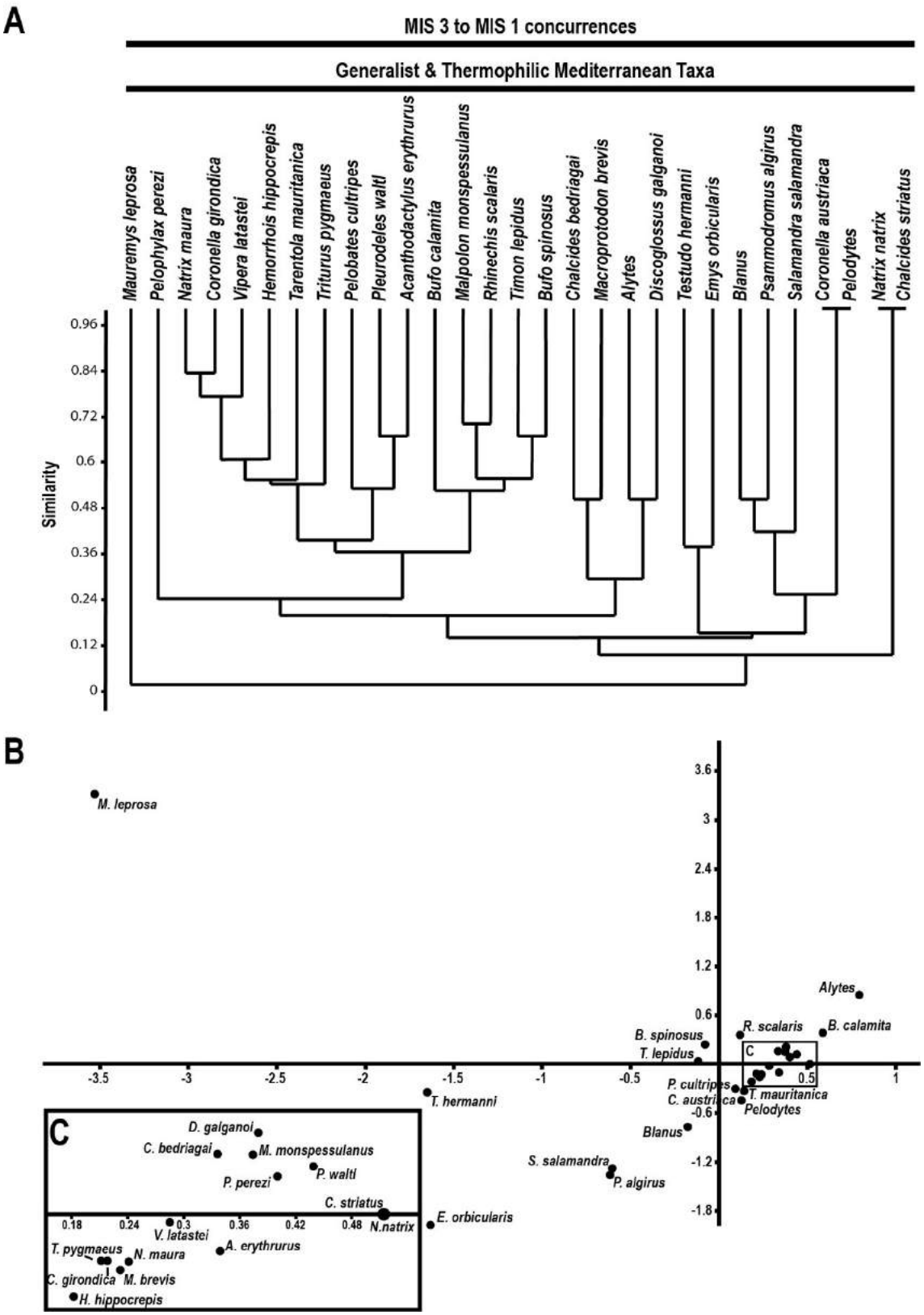

Figure 1.4.- Central and southern Iberian fossil records: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the Correspondence Analysis, with enlarged detail (C), of the latest Pleistocene-Late Holocene assemblages.

which are only represented in the data matrix by citations in assemblages in palaeontological levels, although the quantity of mono-specific citations is higher in the literature. Nonetheless, if these three taxa are excluded, the scenario expounded by the CA allows the existence of a single large group of taxa to be distinguished. The exceptions are the species *S. salamandra* and *Psammodromus algirus* and the genus *Alytes* because of their eccentric positions relative to the other taxa, though they orbit around the main group (Figure 1.4.B). In the case of *P. algirus*, which is an abundant species in the Mediterranean bioregion, this is possibly due to the difficulty of documenting its presence in the fossil record because of the problems in identifying the diagnostic osteological characters, resulting in a small number of citations in the assemblages. In the cases of *S. salamandra* and *Alytes* this may be due to their more hygrophilous tendencies in contrast to the rest of the taxa in the region, which provides a dry and thermophilic context that is in principle less suitable for these amphibians.

Comparing the data with the current situation, in the total of 14 10x10km UTMs where the archaeo-palaeontological sites included in the data matrix of the northern region are located, the following species are present: *Bufo* gr. *B. bufo* (14 assemblages, 100% of the total); *A. fragilis* and *A. obstetricans* (13 assemblages, 92.8%); *L. helveticus* and *N. maura* (12 assemblages, 85.7%); *Pelophylax perezi*, *Podarcis liolepis* and *S. salamandra* (11 assemblages, 78.6%); *Lacerta bilineata*, *N. astreptophora*, *Podarcis muralis*, *R. temporaria* and *Vipera seoanei* (10 assemblages, 71.4%); *Triturus marmoratus* (9 assemblages, 64.3%); *C. striatus*, *Lacerta schreiberi* and *Z. vivipara* (8 assemblages, 57.1%); *C. austriaca* (7 assemblages, 50%); *C. girondica* and *R. iberica* (6 assemblages, 42.8%); *Z. longissimus* and *T. lepidus* (5 assemblages, 35.7%); *E. calamita*, *D. galganoi*, *Hyla molleri* and *I. alpestris* (4 assemblages, 28.6%); *Mauremys leprosa* and *Z. scalaris* (3 assemblages, 21.4%); *Iberolacerta monticola*, *Lissotriton boscai*, *M. monspessulanus*, *P. punctatus*, *Podarcis bocagei*, *P. algirus* and *V. aspis* (2 assemblages, 14.3%); *B. cinereus*, *C. lusitanica*, *Emys orbicularis*, *Rana dalmatina* and *V. latastei* (1 assemblage, 7.1%) (Table 1.2) (based on AHE, 2016).

At present, at a specific level, *Z. vivipara*, the different species of the genus *Podarcis*, *P. algirus*, *H. molleri*, *E. orbicularis*, *M. leprosa*, *B. cinereus*, *V. aspis*, *V. latastei*, *L. boscai*, *P. punctatus*, *P. perezi*, *L. bilineata*, *L. schreiberi* and *I. monticola* have no fossil record in the latest Quaternary in the Cantabrian region. By contrast with its absence in the fossil record, *P. perezi* is notable for its high presence in the current assemblages, although the available genetic studies have not suggested applicable palaeobiogeographical scenarios for the region studied here (Hotz et al., 1994; Arano et al., 1995; Montori, 2014).

In the northeastern region the current situation is very different from the latest Quaternary herpetofauna as known until now, especially for MIS 3. Thus, in the 8 current assemblages located in the same 10x10km UTMs as the sites included in the northeastern area of the Iberian Peninsula, the following

	Northern region		North-eastern region		Central & Southern regions	
	MIS 3 – MIS 1	Today	MIS 3 – MIS 1	Today	MIS 3 – MIS 1	Today
≥ 75% to 100%	*R. temporaria-iberica*	*A. obstetricans* *A. fragilis* *B. spinosus* *L. helveticus* *N. maura* *P. perezi* *P. liolepis* *S. salamandra*		*A. obstetricans* *E. calamita* *B. spinosus* *C. girondica* *M. monspessulanus* *N. maura* *N. astreptophora* *P. punctatus* *P. perezi* *P. liolepis* *P. algirus* *Z. scalaris* *S. salamandra* *T. mauritanica* *T. lepidus*		*E. calamita* *B. spinosus* *M. monspessulanus* *N. maura* *P. perezi* *P. waltl* *P. algirus* *Z. scalaris* *T. mauritanica* *T. lepidus* *V. latastei*
≥ 50% to < 75%		*C. striatus* *C. austriaca* *L. bilineata* *L. schreiberi* *N. astreptophora* *P. muralis* *R. temporaria* *T. marmoratus* *V. seoanei* *Z. vivipara*	*E. calamita* *R. temporaria*	*A. fragilis* *H. meridionalis* *M. leprosa* *P. cultripes* *P. edwardsianus* *V. latastei*	*E. calamita* *B.* gr. *B. bufo* *T. lepidus*	*C. girondica* *H. hippocrepis* *M. leprosa* *N. astreptophora* *P. cultripes* P. *hispanicus*
≥ 25% to < 50%	*Alytes* *A. fragilis* *B.* gr. *B. bufo* *E. calamita* *Vipera*	*E. calamita* *C. girondica* *D. galganoi* *H. molleri* *I. alpestris* *R. iberica* *T. lepidus* *Z. longissimus*	*A. obstetricans* *A. fragilis* *B.* gr. *B. bufo* *C. girondica* *P. punctatus*	*C. striatus* *H. turcicus* *H. hippocrepis* *P. muralis*	*M. monspessulanus* *P. cultripes* *P. waltl* *Z. scalaris* *T. hermanni* *V. latastei*	*A. obstetricans* *B. cinereus* *C. bedriagai* *C. striatus* *D. galganoi* *H. turcicus* *H. meridionalis* *H. molleri* *P. guadarramae* *T. pygmaeus*
< 25%	*C. striatus* *C. lusitanica* *C. austriaca* *C. girondica* *D. galganoi* *H. viridiflavus* *Hyla sp.* *Lacerta* s.l./s.p. *L. helveticus* *M. monspessulanus* *I. alpestris* *N. maura* *N. natrix* s.l. *Z. scalaris* *S. salamandra* *T. lepidus* *T. marmoratus* *Z. longissimus*	*B. cinereus* *C. lusitanica* *E. orbicularis* *I. montícola* *L. boscai* *M. monspessulanus* *M. leprosa* *P. punctatus* *P. bocagei* *P. algirus* *R. dalmatina* *Z. scalaris* *V. aspis* *V. latastei*	*C. asper* *C. austriaca* *M. monspessulanus* *N. maura* *P. cultripes* *Z. scalaris* *S. salamandra* *T. lepidus* *V. aspis* *V. latastei*	*D. pictus* *L. helveticus* *T. marmoratus* *V. aspis* *Z. longissimus*	*A. erythrurus* *Alytes* *Blanus* *C. bedriagai* *C. striatus* *C. austriaca* *C. girondica* *D. galganoi* *E. orbicularis* *H. hippocrepis* *M. brevis* *M. leprosa* *Natrix maura* *N. natrix* s.l. *Pelodytes* *P. perezi* *P. algirus* *S. salamandra* *T. mauritanica* *T. pygmaeus*	*A. erythrurus,* *A. cisternasii* *A. dickhilleni* *C. chamaeleon* *E. orbicularis* *L. schreiberi* *L. boscai* *M. brevis* *P. ibericus* *P. punctatus* *P. hispanica* *P. vaucheri* *P. virescens* *P. edwardsianus* *S. salamandra* *T. marmoratus*

Table 1.2.- Comparison between latest Pleistocene-Late Holocene (MIS3-MIS1) and present-day herpetofaunal assemblages from the same 10x10 km UTMs as the archaeo-palaeontological sites included in the regional data matrices.

species are present: *E. calamita*, *Bufo* gr. *B. bufo*, *M. monspessulanus*, *P. perezi*, *P. liolepis*, *P. algirus* and *T. lepidus* (8 assemblages, 100%); *A. obstetricans*, *N. maura*, *Z. scalaris*, *S. salamandra* and *T. mauritanica* (7 assemblages, 87.5%); *C. girondica*, *N. astreptophora* and *P. punctatus* (6 assemblages, 75%); *A. fragilis* and *V. latastei* (5 assemblages, 62.5%); *Hyla meridionalis*, *M. leprosa*, *P. cultripes* and *Psammodromus edwardsianus* (4 assemblages, 50%); *C. striatus* (3 assemblages, 37.5%); *H. turcicus*, *H. hippocrepis* and *P. muralis* (2 assemblages, 25%); *Discoglossus pictus*, *L. helveticus*, *T. marmoratus*, *V. aspis* and *Z. longissimus* (1 assemblage, 12.5%) (Table 1.2) (AHE, 2016). *P. perezi*, *P. liolepis*, *P. algirus*, *Z. scalaris*, *H. meridionalis*, *P. edwardsianus*, *H. turcicus*, *H. hippocrepis*, *P. muralis*, *D. pictus*, *L. helveticus*, *T. marmoratus* and *Z. longissimus* are species absent from the prehistoric record of the Late Quaternary in the northeastern Iberian area. The turtles *T. hermanni*, *M. leprosa* and *E. orbicularis* have a fossil record in northeastern Iberia during the latest Pleistocene and Holocene, although they are mono-specific citations that have been excluded from the regional data matrix (Mora et al., 2003; Budó et al., 2005; Fèlix et al., 2006; Morales and Sanchis, 2009; Daura and Sanz, 2012).

For the southern and central regions, the following species are present in the nine current assemblages located in the same 10x10 km UTMs as the sites included within the limits of the Spanish State: *E. calamita*, *Bufo* gr. *B. bufo*, *N. maura*, *P. perezi*, *P. algirus*, *Z. scalaris* and *T. lepidus* (9 assemblages, 100%); *M. monspessulanus* and *T. mauritanica* (8 assemblages, 88.89%); *P. waltl* and *V. latastei* (7 assemblages, 77.78%); *C. girondica*, *H. hippocrepis*, *M. leprosa*, *N. astreptophora* and *P. cultripes* (6 assemblages, 66.67%); *Psammodromus hispanicus* (5 assemblages, 55.55%); *B. cinereus*, *Chalcides bedriagai*, *D. galganoi*, *H. turcicus* and *H. molleri* (4 assemblages, 44.44%); *A. obstetricans*, *C. striatus*, *H. meridionalis*, *Podarcis guadarramae* and *Triturus pygmaeus* (3 assemblages, 33.33%); *A. erythrurus*, *E. orbicularis*, *L. schreiberi*, *Macroprotodon brevis*, *Pelodytes ibericus*, *P. punctatus*, *Podarcis hispanica*, *Podarcis vaucheri*, *Podarcis virescens*, *P. edwardsianus*, *S. salamandra* and *T. marmoratus* (2 assemblages, 22.22%); *Alytes cisternasii*, *Alytes dickhilleni*, *C. chamaeleon* and *L. boscai* (1 assemblage, 11.11%) (Table 1.2) (AHE, 2016).

The different species of the genera *Podarcis* and *Hyla*, as well as the species *A. dickhilleni*, *A. obstetricans*, *H. turcicus*, *L. schreiberi*, *L. boscai*, *P. ibericus*, *P. edwardsianus*, *P. hispanicus* and *T. marmoratus*, are without citations at a specific level in the central-southern fossil record for the period between MIS 3 and MIS 1.

1.4. Discussion

1.4.1. *Northern region*

The most representative taxa for the prehistoric sequence of the end of the Upper Pleistocene and Holocene in the northern Iberian area, which ranges from Navarre to Galicia, are *Bufo* gr. *B. bufo*, *E. calamita*, *R. temporaria* (or *R. temporaria-iberica*), *A. fragilis* and the genera *Alytes* and *Vipera*, which are a typical assemblage in forest environments and wet meadows with abundant water points.

A. fragilis is a legless lizard widely distributed across Euro-Siberian Europe, which extends significantly into the northern portion of the Iberian Peninsula. It is a hygrophilous species that occupies a wide range of habitats typical of the Euro-Siberian region, especially those with a dense herbaceous stratum, although it may occasionally appear in the supra-Mediterranean and oro-Mediterranean bioclimatic levels of the Iberian Mediterranean area (Galán and Salvador, 2009), provided that the average annual rainfall exceeds 600 mm (Llorente et al., 1995). Also, its presence is negatively correlated with the number of annual hours of sunshine and with the average temperature of the warmest month, for it prefers cooler and wetter areas with the rainfall distributed throughout the year (Smith, 1998). *B. spinosus* (the Iberian species of the *Bufo* gr. *B. bufo* clade) currently prefers the forested areas of the northern Iberian area, deciduous forests with the presence of water courses and, to a lesser extent, wet meadows (Ortiz-Santaliestra, 2014). *R. temporaria* limits its distribution range to areas with temporary or permanent water points (Álvarez, 2014) and it depends on an average annual rainfall that exceeds 1,100 mm in the eastern Cantabrian area (Gosá and Bergerandi, 1994).

The documented assemblages dating from MIS 3 and MIS 2 in northern Iberia stand out for the low variety of identified taxa: *S. salamandra*, *A. obstetricans*, *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria-iberica*, *A. fragilis* and *Vipera* sp. (Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b; López-García et al., 2011c; García-Ibaibarriaga et al., 2015), in addition to the citations of Ophidia indet. (López-García et al., 2010b), Colubrinae indet. (Martín et al., 2009) and Salamandridae indet. (Zubeldia et al., 2007). Compared to MIS 3, the fossil record of MIS 2 is thus notable for the absence of fossil remains from Salamandridae and Colubridae, as well as the presence of a single record of the genus *Vipera* in the fossil record for the northern area (López-García et al., 2010b). *A. fragilis*, which is widely represented in the sequences of MIS 3 and MIS 1, is only found in level Arg-0 of Santimamiñe (Murelaga et al., 2011) and level C of Antoliñako Koba (Zubeldia et al., 2007). The typical association is reduced to *A. obstetricans*, *E. calamita*, *Bufo* gr. *B. bufo* and *R. temporaria-iberica* (Esteban and Sanchiz, 1985; Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b; Murelaga et al., 2011), with sporadic records of *A. fragilis* (Zubeldia et al., 2007; Murelaga et al., 2011), *Vipera* sp. (López-García et al., 2010b), Lacertidae indet. (cf. *Podarcis*) (Zubeldia et al., 2007; López-García et al., 2010b) and the probable *R. dalmatina* from Erralla VI (Esteban and Sanchiz, 1985).

The species present before and during the Last Glacial Maximum are mostly generalist species that can tolerate a wide climatic and environmental spectrum (*Bufo* gr. *B. bufo*, *E. calamita*, *A. fragilis* and the genera *Rana* and *Vipera*). Significantly, the northern sequence is monopolized by *R. temporaria*, a species that has a pronounced preference for humid environments and Euro-Siberian climatic conditions, and this frog species appears in all of the documented assemblages in the sequences of MIS 3 and MIS 2.

In the fossil record, significant changes are detected in the composition

of herpetofaunal associations from the beginning of MIS 1. In some assemblages the number of hygrophilous and generalist species increases, while species linked to a Mediterranean influence appear in this area for the first time. The first citation of a thermophilic species in the fossil record of northern Iberia during the postglacial period is the snake *M. monspessulanus* in the Lower Unit of Valdavara-1 (15,120±70 BP-13,770±70 BP, Vaquero et al., 2009; López-García et al., 2011b). These absolute datings situate the Lower Unit of Valdavara-1 in the warm climate phase of the Bölling-Allerød interstadial (Naughton et al., 2015) and are consistent with the presence of *M. monspessulanus*. This is a fully thermophilic snake with high thermal requirements (Cheylan et al., 1981; Blázquez and Pleguezuelos, 2002), whose appearance in the Galician area can be related to a process of colonization of the northern region from a southern Iberian *refugium* due to the rising temperatures after the end of MIS 2.

The latest Pleistocene sequence in the Lower Unit of Valdavara-1 also features the first appearance of the snakes *N. maura*, *N. natrix* (sensu lato) and *C.* cf. *austriaca* and the reappearance of *S. salamandra*, which is absent in MIS 2. Further, in this same unit the genus *Lacerta* (sensu lato) is cited for the first time in the regional record of the Late Pleistocene (López-García et al., 2011b). This is an interesting citation given that Lacerta sensu lato in the northern area includes three diferent species (*T. lepidus*, *L. schreiberi* and *L. bilineata*), which underwent three different processes of postglacial colonization according to molecular data from the Cantabrian fringe (Paulo et al., 2001, 2002a; Guedes, 2015). Therefore, greater efforts or news sub-fossil discoveries are required for their species-level assignment.

In the eastern part of the Cantabrian fringe, in the Basque Country, the three levels with herpetofaunal assemblages from Cueva de Santa Catalina, and especially levels N.II and N.I, stand out for the high diversity of their assemblages in the early Pre-Boreal stage of the Holocene (Bailon and García-Ibaibarriaga, 2014). The newt cf. *I. alpestris* has its first record in level N.III in the final phase of the latest Pleistocene (between 12,425±90 BP and 12,345±85 BP), while in the Holocene level N.II (11,155±80 BP) and level N.I (between 10,530±110 BP and 9,180±110 BP) (Arribas and Berganza, 2010) some species previously absent from the prehistoric sequence of the Late Pleistocene appear in concurrence: cf. *L. helveticus*, *Triturus* cf. *marmoratus*, *C. striatus*, *C.* cf. *girondica*, cf. *Z. longissimus* and cf. *H. viridiflavus*. *Lacerta* sp. (= *Lacerta* sensu lato) also appears in both Holocene levels from Santa Catalina, with the same taxonomic problems as in the aforementioned case of the Lower Unit of Valdavara-1. The frog *Hyla* sp., an unprecedented genus in the regional record, appears in level N.II of Santa Catalina (Bailon and García-Ibaibarriaga, 2014).

Levels N.II and N.I of Santa Catalina provide two rich assemblages of species that currently have diverse biogeographical dynamics, which might suggest multiple colonizations in the Cantabrian area from distant and different *refugia*. However, the case of *L. helveticus* invokes caution with respect to these hypotheses. This newt is distributed from the northern third of

the Iberian Peninsula to the northern tip of Great Britain and the extreme west of the Czech Republic (Schlüpmann and van Gelder, 2004). Molecular analyses have identified great genetic diversity among its Iberian populations, which are grouped into four different clades. It was exclusively the eastern clade of *L. helveticus* that carried out the postglacial colonization of Western and Central Europe, the Iberian Peninsula thus serving as its glacial refuge (Recuero and García-París, 2011). These data contrast with the apparent absence of *L. helveticus* in the northern fossil record of the Late Pleistocene, indicating that its glacial refugia were possibly located in the south.

The herpetofaunal assemblage of the archaeological site of Las Orcillas-1 in Navarre is of a later date. Concretely, the archaeological remains of levels C.II-I from Las Orcillas, which are assigned to the Microlaminar Epipaleolithic and dated to 8,610 ± 50 BP, locate the herpetofaunal assemblage in the late Pre-Boreal stage (Fernández et al., 2010). The association is formed by *Bufo* gr. *B. bufo*, *E. calamita*, *T. lepidus*, *M. monspessulanus*, *Natrix* sp. and *Zamenis-Rhinechis* (= *Elaphe* sp. sensu lato) (Fernández et al., 2010). This assemblage includes two thermophilic Mediterranean species, the lizard *T. lepidus* and the snake *M. monspessulanus*, this being the oldest Holocene record for *T. lepidus* in the northern Iberian Peninsula. It also includes the possible presence of other species typical of warm environments, such as *Z. scalaris*.

At the western end of the northern Iberian region, in Galicia, the Upper Unit of Valdavara-1 also presents a more recent assemblage with the presence of thermophilic Mediterranean species. The Upper Unit is ascribed to the Chalcolithic and is dated to 4,490 ± 40 BP (Vaquero et al., 2009). The assemblage from this level is formed by *C. lusitanica*, *Discoglossus* cf. *galganoi*, *Bufo* gr. *B. bufo*, *R. iberica*, *C. striatus*, *A. fragilis*, *T. lepidus*, *N. maura*, *Coronella* cf. *austriaca*, *M. monspessulanus* and *Vipera* sp. (Blain et al., 2009b; López-García et al., 2011b). The frog *R. iberica*, an Iberian endemism that is ecologically very similar to *R. temporaria*, has its oldest record in level 1 of Cueva Millán, dated to MIS 3 (Esteban and Sanchiz, 1990; Díez et al., 2008), and reappears during MIS 1 in the Upper Unit of Valdavara-1. *M. monspessulanus* and *T. lepidus* appear again in association in the Upper Unit of Valdavara-1, also accompanied by another thermophilic species that makes its first postglacial appearance in the northern region, the frog *D. galganoi* (López-García et al., 2011b). *C. lusitanica* also appears for the first time in this region; this is a salamander whose distribution is currently limited to northwestern Iberia (Blain et al., 2009b). Another species typical of this region has been identified in the Upper Unit of Valdavara-1, the skink *C. striatus* (López-García et al., 2011b), which is also present in levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014). The genus *Lacerta*, which has no fossil record with specific-level ascription in the Atlantic-Cantabrian region, includes another reptile typical of northwestern Iberia, *L. schreiberi*, as well as *L. bilineata* for the northern area. Large-sized lizards assigned to *Lacerta* sp. have been identified in the Lower Unit of Valdavara-1 (López-García et al., 2011b)

and level 1 of Cobrante (Martín et al., 2009).

The prehistoric assemblages from Orcillas-1 and Valdavara-1 possibly indicate the existence of two colonization routes towards the north of the Iberian Peninsula for species of Mediterranean influence and for hygrophilous species less tolerant to cold climates and glacial conditions. The eastern route, represented by Orcillas-1, would consist of the Ebro Valley and, according to the fossil record, would have been used by a Mediterranean herpetofauna (e.g., *T. lepidus*, *M. monspessulanus* and possibly *Z. scalaris*). The western route, marked by Valdavara-1, would be located on the Atlantic coastline running towards the Galician coasts and would have been used by species of Mediterranean origin (e.g., *D. galganoi*, *T. lepidus* and *M. monspessulanus*) as well as typically western species (e.g., *C. lusitanica* and *L. schreiberi*), and generalist species and/or species tolerant to Euro-Siberian conditions (e.g., *N. maura* and *C. striatus*), to colonize north-western Iberia and the Cantabrian fringe.

Given our imperfect knowledge of the fossil record, molecular genetics is a discipline that can clarify expansive movements during postglacial colonization. Molecular studies of current populations of *C. lusitanica* are consistent with the proposed scenario, with two clades separated by the Mondego river, it being the northern population that underwent a postglacial expansion towards Galicia and Asturias (Alexandrino et al., 2000, 2002, 2005, 2007). The data provided by mitochondrial DNA show the existence of four clades of *L. schreiberi*. The northwestern clade has less genetic diversity and a greater geographical distribution, related to a very rapid recent expansion (Paulo et al., 2001), an expansive colonization process also documented in its nuclear DNA (Godinho et al., 2008). In the northwestern region, a chronologically recent expansive pattern has also been documented in *P. bocagei* (Pinho et al., 2007a). By contrast, *C. striatus* shows two distinct clades, the first distributed in the south of the Iberian Peninsula and the second spanning northern Iberia, the south of France and northwestern Italy. This second clade has a uniform genetic composition with a low level of diversification, which corresponds to a rapid and recent expansion, possibly postglacial (Carranza et al., 2008). *C. girondica* also shows a similar phylogeographic pattern, with three clades in European territory: two clades are limited to the Baetic region and southwestern Iberia, in contrast to the third clade, characterized by low genetic diversity, which covers the rest of the Iberian Peninsula, southern France, and northern and central Italy, and is the result of a recent expansion (Santos et al., 2012). *N. maura* has two well-differentiated clades in the Iberian Peninsula, a southern one based in the extreme south of Andalusia and another clade found in the rest of the Iberian Peninsula, which would have also colonized central and southern France, western Switzerland and northwestern Italy in the course of the Holocene (Joger et al., 2006).

Z. longissimus is another snake that makes its first appearance in the northern area during the Holocene. This also represents its first appearance in the Iberian prehistoric record. Accordingly,

its first record corresponds to levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014), followed by the Aizkoltzo sequence (Murelaga et al., 2008) and the Chalcolithic level of El Mirón (Sanchiz et al., 2012). Phylogenetic analyses have suggested the expansion northwards of *Z. longissimus* during the Holocene Climate Optimum (*ca*. 8000-5000 BP) from two glacial *refugia* separated by the Alps, reaching its maximum latitudinal range in the Danish Peninsula. After this warm climate phase its distribution recoiled southwards, leaving isolated present-day populations in Germany and the Czech Republic (Musilová et al., 2010). In the Iberian Peninsula it has colonized regions of the Pyrenees, in addition to which it has two separate populations, one in the Picos de Europa (Cantabria) and another in the Galician Massif which would be the result of a postglacial colonization and the subsequent retraction of its Iberian distribution (Ayllón et al., 2010; Cabana et al., 2014). The chronology of the Iberian sites with a record of *Z. longissimus*, coupled with the existence of these isolated populations, is consistent with the pattern proposed on the basis of phylogenetic studies (Musilová et al., 2010), although one might advance to the early Holocene the southern expansion of this snake. *H. viridiflavus*, another snake originating from the Italian Peninsula, which appears in levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014), presents a similar phylogeography, although there are no molecular data for the Iberian populations. The closest studied populations are from France; these are the result of a recent colonization from the western Italian clade of *H. viridiflavus* (Nagy et al., 2002).

In contrast, data provided by the genetic studies of other Iberian species make caution essential when drawing conclusions based only on the fossil record as currently known. *Z. vivipara* is a Euro-Siberian lizard with a wide Palearctic distribution (Dely and Böhme, 1984), although in Iberia it is currently restricted to the Cantabrian fringe and the Pyrenees (Braña and Bea, 2002). This distribution pattern, along with its apparent absence from the Iberian fossil record, may suggest a postglacial colonization from Central Europe, where it has a fossil record during the Pleistocene (Holman, 1998). Nevertheless, phylogeographic genetic studies present a diversified situation, with five clades present in its Iberian distribution area, which were generated by vicariant processes throughout the Pleistocene (Milá et al., 2013). Similar phylogeographies are repeated in the case of two lizard taxa with an Iberian distribution, *P. muralis* (Salvi et al., 2013) and the genus *Iberolacerta* (Crochet et al., 2004). This leads us to propose a long evolutionary history within their own territory; apparent absences in the known fossil record are explained by the difficulty of their taxonomic identification from osteological characters (Barahona, 1996; Barahona and Barbadillo, 1997), making greater efforts necessary in this field. These taxa may be behind the indeterminate lizards of levels 9-7, 5 and 2 of Askondo (García-Ibaibarriaga et al., 2015), levels P11-3 and P1 of El Portalón (López-García et al., 2010b), and cf. *Podarcis* of levels D, C and B of Antoliñako Koba (Zubeldia et al., 2007).

During MIS 1 significant changes are detected in the composition of the assemblages of reptiles and amphibians,

though most of them are still dominated by the same species present in the sequences of MIS 3 and MIS 2: *A. obstetricans*, *A. fragilis*, *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria* (or *R. temporaria-iberica*) and the genus *Vipera*. For example, the assemblages of levels IV, III and II of Erralla (Esteban and Sanchiz, 1985), levels *Balm*, *Almp*, *Slnc*, *Arcp*, *Slm* and *Lsm* of Santimamiñe (Murelaga et al., 2011), level 2 of Cobrante (Martín et al., 2009), levels 3 and 2 of Askondo (García-Ibaibarriaga et al., 2015), level A of Antoliñako Koba (García-Ibaibarriaga et al., 2015) and the Bell Beaker level of the dolmen of Errekatxuetako Atxa (Murelaga et al., 2007) are exclusively composed of taxa from the previously mentioned herpetofaunal association.

The midwife toad *A. obstetricans*, with representation through MIS 2 in the sequences from Portalón de Atapuerca (López-García et al., 2010b) and Erralla (Esteban and Sanchiz, 1985), disappears from the fossil record of the Pleistocene part of MIS 1. It then reappears in level N.1 of Cobrante, which is ascribed to the Holocene (Martín et al., 2010). Subsequently, it also appears in the Neolithic and Bronze Age levels of El Mirón (Sanchiz et al., 2012) and in the dolmen of Errekatxuetako Atxa (Murelaga et al., 2007). On an ecological level, this absence, if it genuinely occurred and is not the product of a possible taphonomic bias, could simply be correlated with the absence of permanent water points between Heinrich Event 1 and the Pre-Boreal Holocene stage. Such points are necessary for it to complete its larval stage (Bosch, 2014).

Nonetheless, this is contradicted by the presence of species closely linked to an aquatic environment such as *S. salamandra*, cf. *I. alpestris* and cf. *L. helveticus* in the latest Pleistocene sequence from Santa Catalina and Laminak II (Sanchiz and Esteban, 1994; Bailon and García-Ibaibarriaga, 2014) and the indeterminate salamander from level B of Antoliñako Koba (Zubeldia et al., 2007).

The toad *E. calamita* had a greater distribution in the palaeontological record than at present. Today its distribution in the Cantabrian area is very scarce and is limited to the southernmost fringe and two coastal populations in the Basque Country (Tejedo and Reques, 1997; Reques and Tejedo, 2002; Garin-Barrio et al., 2007). In the Late Quaternary record, it appears in a total of 20 assemblages: the entire sequence from Portalón de Atapuerca and Santa Catalina (López-García et al., 2010b; Bailon and García-Ibaibarriaga, 2014), levels V and IV of Erralla (Esteban and Sanchiz, 1985), levels Camr-Csn and Lsm of Santimamiñe (Murelaga et al., 2011), level Ll.15-12 of Aizkoltzo (Murelaga et al., 2008), levels C.II-I of Las Orcillas-1 (Fernández et al., 2010) and possibly levels 4 and 3 of Cobrante (Martín et al., 2009). Today *E. calamita* is absent in the vicinity of Cobrante, Aizkoltzo, Erralla, Santimamiñe and Santa Catalina, but present in the territories of Las Orcillas-1 and Portalón de Atapuerca. Nowadats, it is also present in the area around Valdavara-1 and Peña Larga (AHE, 2016), although it does not appear in the archaeological record of these sites.

1.4.2. *North-eastern region*

The dominant species in the latest Quaternary in the northeastern fossil record, which basically includes Catalonia and Aragon, are *A. obstetricans*, *E. calamita*, *R. temporaria*, *A. fragilis* and to a lesser extent *Bufo* gr. *B. bufo*, *C. girondica* and *P. punctatus*. This is an assemblage with hygrophilous tendencies, although the association of *E. calamita* and *P. punctatus* indicates the existence of irregularities in the water regime that may be associated with a Mediterranean influence.

R. temporaria is a Euro-Siberian frog that in the Iberian Peninsula is restricted to the area formed by the axis of the Cantabrian Mountains and the Pyrenees and within the Mediterranean region is only present in the Montseny Massif, due to the latter's Pyrenean influences (Esteban and García-París, 2002). In these regions it lives in wetlands, from mountain meadows to deciduous forests of *Quercus* and *Fagus* (Álvarez, 2014). It does not tolerate ambient temperatures over 26ºC and needs average temperatures below 5°C in autumn and winter to carry out its reproductive cycle (Balcells, 1975). *A. obstetricans* is another anuran especially associated with high rainfall areas. Away from these, its distribution is restricted to mountainous systems or areas that allow permanent water points, because of its particularly long larval development lasting from 91 days to three years (Bosch, 2014). *C. girondica* is a snake with an extensive western Mediterranean distribution and presents great altitudinal and environmental variation, although its main ecological requirement is the presence of small lizards (genera *Psammodromus* and *Podarcis*), its main prey (Santos and Pleguezuelos, 2009). The herpetofaunal taxa present in MIS 3 are mainly generalists and species tolerant to Mediterranean conditions as well as to Euro-Siberian climates. Noteworthy is the practical absence of thermophilic taxa by contrast with the recurrent appearance of *R. temporaria*, despite it being an area in direct contact with the Mediterranean Sea. In fact, *R. temporaria* appears outside its current distribution in the latest Pleistocene sequences of Teixoneres, Abric Romaní and Galls Carboners; this latter site is located 120 kilometers from the current southern boundary of the *R. temporaria* distribution on the Montseny Massif. Further, the Pleistocene citations of *V. aspis* from Teixoneres and Abric Romaní lie outside its current distribution range.

Very common species in the Mediterranean area that have significant fossil records in contemporary sites in southern Iberian areas, such as the lizard *T. lepidus* or the snake *N. maura*, only appear in the northeastern region in the Holocene levels of Balsa la Tamariz (Laplana and Cuenca-Bescós, 1995) and Cova Colomera, respectively (López-García et al., 2010a). The thermophilic Mediterranean gecko *T. mauritanica* also has its only record in this latter cave, in its most recent phase (level A.sup., 3,490 ± 50 BP) (López-García et al., 2010a). The snake *M. monspessulanus*, closely linked to the Mediterranean bioclimate, has its only record in the latest Pleistocene in level IIb of Cova Teixoneres, assigned to MIS 3 (ca. 35,000 BP) (López-García et al., 2012b, 2014a; Talamo et al., 2016). This snake reappears in the northeastern record until the Bronze Age level of Balsa la Tamariz (ca. 3,600-3,400 BP), where appear in concurrence with *T. lepidus* (Laplana and Cuenca-Bescós, 1995). The

thermophilic assemblage from Balsa la Tamariz (*P. cultripes*, *T. lepidus* and *M. monspessulanus*) in the Ebro Valley, combined with the presence of *T. mauritanica* in the last phase from Cova Colomera, located on one of the tributaries of the Ebro river (López-García et al., 2010a), may possibly be correlated with the existence of a natural corridor along the Ebro Valley and its tributaries, from which species native to the Mediterranean area would have colonized the Iberian inland during the Holocene climatic progression.

For the newt *T. marmoratus*, absent in the regional fossil record, different routes of colonization have been proposed for its two eastern populations: the one located in the province of Girona would be the result of a postglacial colonization from Roussillon on the other side of the Pyrenees, while the populations of southern Catalonia and central Aragon would have come from the Navarra-Rioja area; this species possibly used the Ebro river to colonize as far as its final section (Llorente et al., 1995; Montori, 2014). The Ebro Valley would have thus served as a route running in both directions, for Mediterranean species leading inland towards the north of the Iberian Peninsula and for hygrophilous species from the north leading to the new environments that had opened up on the eastern periphery.

The snake *C. austriaca*, with a record in MIS 3 in levels IIb and II from Cova Teixoneres (López-García et al., 2012b, 2014a) and from Canyars (Daura et al., 2013; López-García et al., 2013, 2014a), is the only species present in the northeastern prehistoric record that does not appear in the current assemblages. Another species of the genus *Coronella*, *C. girondica*, which appears on levels 8 to 5 of Cova Xaragalls (López-García et al., 2012c) and C15, C14-13 and C12 of Cova Colomera (López-García et al., 2010a), is currently distributed in a greater number of assemblages and has a greater distribution range. *C. austriaca* is much less thermophilic than *C. girondica* and the altitudinal and environmental segregation of these two species has been confirmed in the Iberian Peninsula when they are in sympatry (Galán, 1988; Lizana et al., 1988; Morales et al., 2002). The absence of *C. austriaca* in areas where it was present in the past and the currently greater distribution of *C. girondica* can be correlated with altitudinal changes in the bioclimatic levels, as proposed for the sequence from MIS 5c to MIS 4 of Cueva del Camino (semi-arid climate during warm periods to a wet mid-latitude climate during cold periods) (Blain et al., 2014b).

The absence of sites dating from MIS 2 and the poor data from MIS 1 for this area of Iberia preclude a deeper evolutionary comparison of its herpetofauna. However, the ongoing studies of the microvertebrate remains from Cova Bonica, Balma del Gai, l'Arbreda and Coves del Toll will increase what is known of the composition of the herpetofauna record and its main biogeographic changes in the Catalan area during the Late Quaternary. The current herpetofaunal composition of the northeastern region suggests a postglacial recolonization of this territory by thermophilic species along the Mediterranean coast from the Valencian Country and inland through river valleys, especially the Ebro and its tributaries. In parallel, other species would have entered from the north by

the Mediterranean coast and the eastern edge of the Pyrenees, originating from the south of France and the west of Italy, as seen for the Cantabrian region with *Z. longissimus*, *H. viridiflavus* and *L. bilineata*. Finally, native Pyrenean species might have used the same river valleys to penetrate into the Pre-Pyrenean foothills and the Catalan central basins that were favorable for colonization. This would have been in addition to the existence in these mountainous areas of interglacial *refugia* for species from Euro-Siberian and/or Alpine environments, as proposed for Cova Colomera and the Serra del Montsec for species such as *R. temporaria* and *A. fragilis* (López-García et al., 2010a).

1.4.3. *Central and southern regions*

E. calamita, *T. lepidus*, *Bufo* gr. *B. bufo*, *Z. scalaris* and, to a lesser extent, *P. cultripes*, *T. hermanni*, *M. monspessulanus*, *P. waltl* and *V. latastei* are the most-represented species in the palaeo-archaeological sites of the central and southern Iberian Peninsula from MIS 3 to MIS 1. Together they constitute an association of herpetofauna typical of most of the thermophilic environments in current Mediterranean Iberia (with the exception of *T. hermanni*, extinguished regionally). As mentioned above, they form an assemblage with a predilection for dry Mediterranean environments with a markedly seasonal water regime and the presence in the landscape of both open areas and scrubland and forests.

The large lizard *T. lepidus* is one of the most characteristic species of the Mediterranean bioclimate in southwestern Europe, to the extent that the northern boundary of its distribution coincides with the boundary between Mediterranean and Euro-Siberian bioclimates (Cheylan and Grillet, 2005). *B. spinosus* is a very generalist toad that occupies practically all habitats characteristic of the Iberian Peninsula, from the thermo-Mediterranean premontane areas to the Euro-Siberian mountains (Ortiz-Santaliestra, 2014), while *E. calamita*, also generalist and fairly widespread, prefers open areas with sparse vegetation or low cover and high insolation, associated with a higher degree of environmental aridity and higher annual average temperatures (Gómez-Mestre, 2014). The viper *V. latastei* is a species typical of humid, sub-humid and semi-arid Mediterranean climates with a preference for plains and warm areas, rocky areas with scattered vegetation cover, as well as forest glades (Brito, 2011). *P. waltl* is a fully thermophilic newt, and is currently the only salamander present in the eastern Iberian Mediterranean area, where it occupies the thermo-Mediterranean, meso-Mediterranean and supra-Mediterranean bioclimates (Montori et al., 1997, 2002).

Also characteristic of the fossil record of this region is the presence of *T. hermanni*, which during the Late Pleistocene presents a continuous record from the previous interglacial (MIS 5e) until the period before the Last Glacial Maximum (MIS 2), confirming the prehistoric distribution of this land tortoise in the Iberian inland and along the Atlantic coast. These are regions where it is now extinct (Morales and Sanchis, 2009) and *T. hermanni* is currently associated with limited coastal areas with a Mediterranean climate in the northern half of the Iberian Mediterranean coast, although in the

east of its Mediterranean distribution in Italy and the Balkans it also appears in sub-Mediterranean climates, living in open environments, such as glades in wooded areas, shrublands or dune grasslands (Bertolero, 2010). Temperatures mark the viability of *T. hermanni* embryos, which die at temperatures below 25°C or above 35°C (Eendeback, 1995), possibly serving to establish one of its climatic barriers, based on the maximum/minimum temperatures of the months between the egg laying and eclosion from mid-May to early October (Bertolero, 2010).

The association of species typical of the Atlantic Iberian area such as *T. pygmaeus*, *C. striatus* or the genus *Lissotriton* in the Pleistocene levels of Gorham's Cave (MIS 3-1, 32,500-10,800 BP), along with predominantly thermo-Mediterranean faunal and botanical records, suggest the existence of a southern glacial *refugium* for the herpetofaunal species of the western Iberian Peninsula during the most critical climatic phases of the Late Pleistocene, within their parameters of habitability but outside their current distribution areas (Blain et al., 2013). A clear example of this approach is the current absence of the genus *Lissotriton* in the Iberian part of the Strait of Gibraltar, the *L. boscai* populations of the Doñana National Park being the closest to Gorham's Cave, which is located more than 120 kilometers away (Díaz-Paniagua, 2002). This raises the possibility that there was first an expansion of its distribution towards the south during the last glacial phase and subsequently a retraction of the populations towards the north during the Holocene.

The continued presence of the gecko *T. mauritanica* is significant from the previous interglacial (MIS 5), with the sequence from Vanguard's Cave (Gleed-Owen, 2001; Gleed-Owen and Price, 2012), to the present, with records ranging from MIS 3 to MIS 1 in the sequences from Boquete de Zafarraya and Gorham's Cave (Barroso and Bailon, 2003; Barroso et al., 2003; Blain et al., 2013). This fossil record confirms its indigenous Iberian character from prior to the Holocene and contradicts the theory of its introduction by humans in recent times (Mayol, 1985; Harris et al., 2004a). This also coincides with the genetic diversity of the *T. mauritanica* populations observed in central and southeast Iberia, with three different lineages identified (Harris et al., 2004b; Perera and Harris, 2008), the central populations presenting an old mitochondrial lineage that refutes the theory of its recent introduction and corroborates its autochthony, at least in the case of these central populations. In fact, the genetic distance among the Iberian populations of *T. mauritanica* is so high that it could possibly be ascribed to two different species, the native central species and a recently introduced species on the southern and eastern littoral (Rato et al., 2016). As yet, there is no description of osteological characters that would make it possible to differentiate between these two new species. The absence of *H. turcicus*, the other gecko currently present in the Iberian Peninsula, in the fossil record of the Late Pleistocene and the genetic homogeneity of its European populations, including the Iberian populations, raise the possibility of a very rapid dispersion from a point of origin in the eastern Mediterranean Sea in recent

times and possibly caused by humans (Carranza and Arnold, 2006; Mateo et al., 2011). Later, it would have colonized the Iberian Peninsula from a bridgehead in North Africa, although the mitochondrial homogeneity of the European clade (clade A) may be due to selective sweep processes and not just a recent expansion (Rato et al., 2011). However, it should be noted that *H. turcicus* is a small gecko with a fragile osteology that may suffers problems of preservation in the fossil record.

The herpetofaunal assemblage of level A of Sala de las Chimeneas from Cueva de Maltravieso in Extremadura, dated to the final phase of the Last Glacial Maximum (between 19,500-18,700 cal. BP and 19,700-18,750 cal. BP) (Bañuls-Cardona et al., 2012), is composed of *Bufo gr. B. bufo*, *E. calamita*, *P. perezi*, *T. lepidus*, (cf.) *N. maura*, *C. girondica* and *V. latastei*, an association that shows the survival of a thermophilic Mediterranean herpetofauna within the Iberian Peninsula even in the most critical glacial times of the latest Pleistocene. The herpetofaunal fossil record of central and southern areas is rich if compared with the other two regions analyzed, even though the central area is lower in the number of species than the Andalusian and Portuguese regions. This is the case with the MIS 1 sequence from Peña de Estebanvela prior to the Younger Dryas, with the concurrence of the anurans *Alytes* sp. and *E. calamita* in level VI (14,450 ± 80 BP and 14,200 ± 50 BP) or only *E. calamita* in levels IV, III and II during the Younger Dryas (12,530 ± 60 BP to 11,400 ± 120 BP) (Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013). However, in level I of Estebanvela de Peña, dated at between 11,330 ± 50 BP and 10,640 ± 60 BP, there appears the association of *E. calamita*, *T. lepidus*, *M. monspessulanus*, *Z. scalaris*, (cf.) *Coronella* sp. and *V. latastei*, similar to that documented in level A of Sala de las Chimeneas. In this case it is an assemblage of a markedly Mediterranean herpetofauna occurring at a level assigned to the cold climatic phase of the Younger Dryas. Both cases, level A of Sala de las Chimeneas and level I of Peña de Estebanvela, seem to indicate a climate scenario that is less aggressive than might have at first been thought for the thermophilic and/or typical Mediterranean species of the Iberian inland during the latest Pleistocene. Another thermophilic assemblage dating to MIS 2 is that documented in level IV of Cueva Higueral de Valleja (18,300 ± 4,800 BP and 15,500 ± 3,700 BP), in the region of Cadiz, where appear in concurrence *E. calamita*, *T. mauritanica*, *N. maura*, *M. monspessulanus*, and *Z. scalaris* (Jennings et al., 2009).

In the eastern Mediterranean strip of the studied area, the herpetofaunal fossil record of the Valencian Country is characterized by the scarcity of publications of prehistoric assemblages and the high degree of mono-specific citations in the literature, which is basically monopolized during the Late Pleistocene by *T. hermanni* and *Testudo* sp. (Morales and Sanchis, 2009; Sanchis et al., 2015), a species easily identifiable in the zooarchaeological record by contrast with the non-chelonian herpetofauna. Thus, in the Late Pleistocene of the Valencian Country, this typically Mediterranean turtle is documented in the MIS 5e levels of Cova de Bolomor (Fernández Peris, 2007; Blasco, 2008), the Mousterian levels of Cova Negra of Xàtiva (Pérez Ripoll, 1977), in Abrigo de

la Quebrada (Sanchis et al., 2013), Abric del Salt (Morales and Sanchis, 2009; Pérez Luís, 2014), Abric del Pastor (Galván et al., 2008; Sanchis et al., 2015), San Luís of Buñol (Fernandez Peris and Martínez Valle, 1989) and the Pleistocene sequence of Cova Canet of Aielo de Malferit (Morales and Sanchis, 2009). Further, the presence of indeterminate chelonians is recorded in the Cova de Dalt Tossal de la Font of Vilafamés, possibly associated with an accumulation caused by a group of hyenas (Saladié et al., 2010). In addition to *T. hermanni*, the presence of the toad *Bufo* gr. *B. bufo* (Luis Perez, 2014) has also been identified in level X of Abric del Salt. In the Valencian Pleistocene record, there is evidence of the human consumption (by *H. neanderthalensis*) of turtles in Bolomor, Abrigo de la Quebrada and Abric del Pastor (Blasco, 2008; Galván et al., 2008; Sanchis et al., 2013, 2015).

As regards the Valencian Holocene, citations of the presence of *Testudo* sp. from the Chalcolithic archaeological site of Ereta del Pedregal (Pérez Ripoll, 1990) have recently been assigned to *M. leprosa* and Emydidae/Geoemydidae indet. (Morales and Sanchis, 2009). An individual belonging to *M. leprosa* has also been identified in the Neolithic levels of Cova de l'Or (Pérez Ripoll, pers. com.). In Lloma de Betxí, dated to between 2100 cal. B.C.E. and 1600 cal. B.C.E. and assigned to the Valencian Bronze Culture (De Pedro, 2004), *Bufo* gr. *B. bufo*, *M. leprosa*, *T. lepidus* and *Elaphe* sp. have been identified in concurrence (Tormo and De Pedro, 2013); this latter taxon may be *Z. scalaris*, the only species from the complex of the genus *Elaphe* sensu lato that is present in the Valencian Country, which also includes *Z. longissimus* (Pleguezuelos, 2009; Rubio and Gosá, 2010). *M. leprosa* is also documented in phase III of the Bronze Age from Pic dels Corbs, dated to between 1,400 / 1,350 cal. B.C.E. and 1,100 / 1,050 cal. B.C.E. (Barrachina and Sanchis, 2008).

The prehistoric herpetofauna known from the final Late Pleistocene and the Late Holocene of the Valencian Country is quite poor when compared with the rest of the Iberian Peninsula, both in the number of sites with a published record and in the number of taxa identified, by contrast with the relatively good knowledge of its archaeological record. Assemblages such as those from Lloma de Betxí with *Bufo* gr. *B. bufo*, *M. leprosa*, *T. lepidus* and *Elaphe* sp. (= *Z. scalaris*?) and the combination of *T. hermanni* and *Bufo* gr. *B. bufo* from Abric del Salt represent exceptions within the Valencian herpetofaunal fossil record.

The Portuguese Atlantic region also suffers from a scarcity of sites with a published prehistoric herpetofauna for the period studied. However, by contrast with the Valencia Country, two Portuguese sites have assemblages with a significant number of species: Gruta da Figueira Brava (MIS 3) and Guia de Albufeira (Pleistocene phase of MIS 1) (Crespo et al., 2000; Crespo, 2002). In both herpetofaunal associations there are typically thermophilic species such as *B. cinereus-mariae*, *T. lepidus* and *P. cultripes*, along with other species such as *P. waltl* and *A. erythrurus*, which also have a fossil record in the Andalusian Late Pleistocene. In addition, there are chelonian citations from Gruta Nova da Columbeira (*T. hermanni* and Emydidae indet., MIS 3), Gruta do Caldeirão (*T. hermanni* and *M. leprosa*, MIS 2) and

Gruta do Escoural (*T. hermanni*, MIS 2), as well as the turtle assemblage from Gruta da Figueira Brava (*T. hermanni* and *E. orbicularis*, MIS 3) (Crespo et al., 2000; Crespo, 2002; Morales and Sanchis, 2009; Nabais, 2012).

Apart from its appearance in Gruta do Caldeirão, *M. leprosa* does not have a known record for MIS 3 and 2 in the Iberian Peninsula. However, the number of citations of this turtle increases greatly during the Holocene, above all from the Neolithic onwards (Jiménez Fuentes, 1986; Budó et al., 2005; Félix et al., 2006; Barrachina and Sanchis, 2008; Morales and Sanchis, 2009; Tormo and de Pedro, 2013). In contrast, the other freshwater Iberian turtle, *E. orbicularis*, has a greater number of Late Pleistocene records, namely in the Mousterian sequences from Figueira Brava and Gruta Nova da Columbeira (Emydidae indet.), level IV of Gorham's Cave (Emydidae indet.) and level NM14 of Cueva de Nerja (Jiménez Fuentes, 1986; Gómez and Jiménez Fuentes, 1998; Crespo, 2002; Blain et al., 2013). Genetic studies of current Maghrebian and Iberian populations of *M. leprosa* suggest that it recently colonized the Iberian Peninsula from populations to the north of the Atlas Mountains or even from a bridgehead at the southern tip of the Iberian Peninsula itself, because the Strait of Gibraltar was possibly not an impermeable barrier to genetic exchange between trans-Mediterranean populations of freshwater turtles (Fritz et al., 2006; Velo-Antón and Pinya, 2015a). The genetic scenario amongst the Iberian populations of *E. orbicularis* is much more diverse, with four different clades identified, at least one of them endemic. Of the remaining three, one appears on both sides of the Strait of Gibraltar and the other two clades have eastern and trans-Pyrenean origins and appear in the northern half of the Iberian Mediterranean coast and the Ebro Valley (Velo-Antón et al., 2015; Velo-Antón and Pinya, 2015b). Therefore, the data provided by genetic studies are consistent with the scenario presented by the fossil record, with the possible extinction of *M. leprosa* from most (or even all) of the Iberian Peninsula, while *E. orbicularis* maintained populations in Iberia during the Late Quaternary, being a much less thermophilic species than *M. leprosa*. The onset of the current interglacial would have allowed *M. leprosa* to recolonize the Iberian Peninsula from the Straits of Gibraltar, as well as permitting the arrival of new populations of *E. orbicularis* from the Maghreb and trans-Pyrenean Europe.

As regards species with no fossil record between MIS 3 and MIS 1, there are citations of *Alytes* sp. and *Lissotriton* sp. from Gorham's Cave (Blain et al., 2013) and of *Alytes* sp. from Peña de Estebanvela (Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013), which by their geographical distribution could correspond to *A. cisternasii*/*dickhilleni* and *L. boscai* and to *A. obstetricans*/*cisternasii*, respectively. *H. meridionalis* could have its last Pleistocene fossil record in the Mousterian levels from Vanguard's Cave of Gibraltar, dated to MIS 5 (Gleed-Owen, 2001; Gleed-Owen and Price, 2012), therefore being absent from the rest of the Pleistocene and from the sites hitherto known for the Holocene, when it could have crossed the Strait of Gibraltar to colonize southwest Iberia (Tejedo and Reques, 2002).

Finally, another species of North African origin, *C. chamaeleon*, has a

single zooarchaeological record in the Bronze Age levels of Cueva de la Victoria of Málaga (Talavera and Sanchiz, 1983), being absent throughout the rest of the fossil record of the Iberian Quaternary. This has not been included in the regional data matrix because it is a mono-specific citation. The statistical methods applied to the regional data matrix suggest a scenario of great stability in the herpetofaunal composition of the center and south of the Iberian Peninsula, with little observable change by chronological level. Climatic and environmental changes linked both to the last glacial phase and the subsequent interglacial onset seem not to have had large impacts on the herpetofaunal composition of this area. The detected biogeographic changes are the contraction of the southern boundary in the distribution of some taxa (e.g., genus *Alytes* and *L. boscai* in the Gibraltar region), the possible recolonization by *M. leprosa* from the Maghreb, and the entry of new species such as *H. meridionalis* and *C. chamaeleon*, also from North Africa. In the future, data on the prehistoric herpetofauna of central and southern Iberia are expected to increase from the ongoing study of significant sites such as Pinilla del Valle and new campaigns in the caves of Gibraltar, Castillejo del Bonete and Maltravieso.

1.4.4. *General discussion*

The apparent absence of some species in the fossil record, especially those of smaller size, may be due to multiple factors of destruction and selection, processes also observed in the bias towards specific skeletal elements (Esteban and Sanchiz, 1985). At an ecological level, the lack of specialized predators of particular species of amphibians and reptiles reduces the taphonomic bias generated by them to criteria such as the size of prey or individual visibility at hunting time (Blain, 2009), which may generally affect species of smaller sizes.

One of the most difficult groups when it comes to species-level taxonomic identification is Lacertidae, especially the species of small size, which includes the genera *Podarcis* and *Psammodromus*. *Podarcis* is a lizard genus that currently shows a large specific diversity, manifest in its phylogenetic complexity in the Iberian Peninsula (Kaliontzopoulou et al., 2011). Within this genus, *P. hispanica* (sensu lato) is a paraphyletic taxon that groups most of the rupicolous Iberian lizards, with a distribution that covers most of the Iberian Peninsula up to the isotherm of 14ºC and with significant insolation requirements (Sá-Sousa and Pérez-Mellado, 2002). With the advance of molecular investigations into this taxon, at least six news species have been separated and described, *Podarcis carbonelli*, *P. bocagei*, *P. vaucheri*, *P. liolepis*, *P. guadarramae* and *P. virescens* (Harris and Sá-Sousa, 2001, 2002; Harris et al., 2002; Pinho et al., 2003, 2006, 2007b, 2008, 2009; Renoult et al., 2010; Geniez et al., 2014). Thus, *P. hispanica* sensu stricto is restricted to the Mediterranean eastern area and southeastern Iberia (Geniez et al., 2007). Genetic analyses show that this varied and extensive speciation was the result of a rapid process of allopatric diversification that occurred in a short time period, with different lineages that appeared in relatively small geographical areas. This scenario is associated with the existence of "*refugia within glacial refugia*" in the Iberian Peninsula (Pinho

et al., 2007a), a vicarious regionalization of the Iberian distribution of these species in accordance with the different climatic conditions and geographical barriers.

With a currently poor fossil record that precludes an archaeo-palaeontological approach because of the lack of criteria for taxonomic identification based on the skeletal remains of these new, recently described species, the correlation between the current distribution of the *P. hispanica* complex, the theoretical expansions during the postglacial period and the geographical disposition of their glacial *refugia* can be used to locate those regions that kept optimal climatic conditions for these relatively thermophilic lizards through the different Pleistocene glaciations. Furthermore, a better genetic understanding of the Iberian populations of *P. muralis*, a different species of lizard that is not part of the *P. hispanica* complex, as well as the determination of better osteological characters that may lead to its taxonomic identification in the fossil record, would permit a comparative scenario between these two taxa, since *P. muralis* is a lizard that is much more resistant to Euro-Siberian conditions, which a priori would allow greater adaptability and a wider distribution during the Pleistocene cold phases.

Currently, *P. muralis* occupies the Iberian Euro-Siberian fringe, but also presents two southern relict populations limited to the Central System and the Iberian System mountain ranges that are isolated from the northern populations (Pérez-Mellado, 2002; Diego-Rasilla, 2009), suggesting a greater distribution in the past. At the moment, the data available from its Iberian populations suggest the existence of two endemic clades, clade 2 in the Cantabrian Mountains and clade 3 in the Central System and the Iberian System, plus a third clade in the Pyrenees which is also distributed in western France (clade 1). Furthermore, it has been found that the discontinuity in the distribution of its Iberian populations does not correspond to a genetic discontinuity, so the fragmentation process is due to recent dynamics (Salvi et al., 2013), which can be associated with the effects of climate change in the current interglacial. Two other lizards linked to Euro-Siberian climates and/or to Alpine environments, which show phylogeographies that suggest a long evolutionary history in the Iberian Peninsula, are *Z. vivipara* and the genus *Iberolacerta* (Crochet et al., 2004; Milá et al., 2013) although these have not been identified in the fossil record to date.

Another Iberian lizard, *L. schreiberi*, has four distinct lineages, two coastal clades located on the northern and southern Atlantic littoral, and two inland clades present in the Central System and in the populations of the southern mountain ranges, respectively. These inland clades and the southern coastal population are associated with possible glacial *refugia* for this lizard, the northern coastal lineage being the only one that presents an expansive distribution during the postglacial (Paulo et al., 2001, 2002a). By contrast, processes of genetic divergence reflecting east-west allopatry have been described for Iberian populations of *P. waltl*, *P. algirus*, *A. erythrurus* and *D. galganoi*, associated with the existence of two favorable climatic areas serving the function of a glacial *refugium* in southeastern and

southwestern Iberia (Schmitt, 2007). In contexts beyond the reach of "classic" zooarchaeological studies due to the limitations of a purely osteological taxonomy, molecular studies provide an open window onto the distribution of species in the past and their palaeoclimatic and palaeoenvironmental implications, always bearing in mind the difficulty of reading and dating the genetic isolation of herpetofaunal populations.

The herpetofaunal fossil record of the Iberian latest Quaternary is very rich and varied in comparison with contemporaneous associations documented in Central Europe, which has associations of *S. salamandra*, *Triturus cristatus*, *Triturus vulgaris*, *Bufo bufo*, *Bombina bombina*, *Hyla arborea*, *Pelobates fuscus*, *R. dalmatina*, *R. temporaria*, *Pelophylax ridibunda*, *E. orbicularis*, *A. fragilis*, *Lacerta viridis*, *N. natrix* and *Z. longissimus* during the interglacial optimum, joined in the colder stages of the interglacial by the species *E. calamita*, *Bufotes viridis*, *Rana arvalis*, *L. agilis* and *C. austriaca*, together with *T. vulgaris*, *B. bufo*, *H. arborea*, *P. fuscus*, *R. temporaria*, *P. ridibunda*, *A. fragilis* and *N. natrix*. This herpetofaunal diversity is reduced drastically with the onset of the glacial phase, with associations of *B. viridis*, *R. temporaria*, *Z. vivipara* and *Vipera berus* reported, and finally only the frog *R. temporaria* in the glacial maximum (Böhme, 1996, 2000; Böhme, 2010).

The Iberian scenario shows the continued presence of thermophilic species in the center and south of the Iberian Peninsula and their survival in the most critical moment of the last glacial phase (Figure 1.5), the Last Glacial Maximum, with a typical Mediterranean assemblage of *Bufo* gr. *B. bufo*, *E. calamita*, *P. perezi*, *T. lepidus*, (cf.) *N. maura*, *C. girondica* and *V. latastei* in level A of Sala de las Chimeneas from Cueva de Maltravieso (Bañuls-Cardona et al., 2012). Another pleniglacial herpetofaunal assemblage that is richer than the Central European scenario has also been cited in northern Iberia, with the association of *A. obstetricans*, *Bufo* gr. *B. bufo*, *E. calamita*, *R. temporaria*, Lacertidae indet. and *Vipera* sp. in sub-level 4 of El Portalón de Atapuerca, also dating from the Last Glacial Maximum (López-García et al., 2010b).

Another possible comparison is with the rodent fossil record of the Iberian latest Quaternary, which is characterized by the appearance of most current species, such as *Chionomys nivalis* and *Iberomys cabrerae*, the extinction of *Pliomys lenki*, *Iberomys brecciensis* and *Allocricetus bursae* as well as the disappearance of the Iberian populations of *Microtus oeconomus*, *Microtus gregalis*, *Castor fiber* and *Hystrix brachyura* (Sesé and Sevilla, 1996; López-García, 2008). The emergence of new rodents such as *Mus spretus*, *Mus musculus*, *Micromys minutus*, *Rattus rattus* and *Rattus norvergicus* occurred throughout the Holocene, and these are species related to humans by commensalism (Sesé and Sevilla, 1996). By comparison, among reptiles and amphibians the scenario is more static and limited to the glacial restriction of thermophilic and/or Mediterranean taxa to central and southern Iberia, with the subsequent colonization by some of these species of the northern Iberian regions taking advantage of the postglacial climate improvement, but

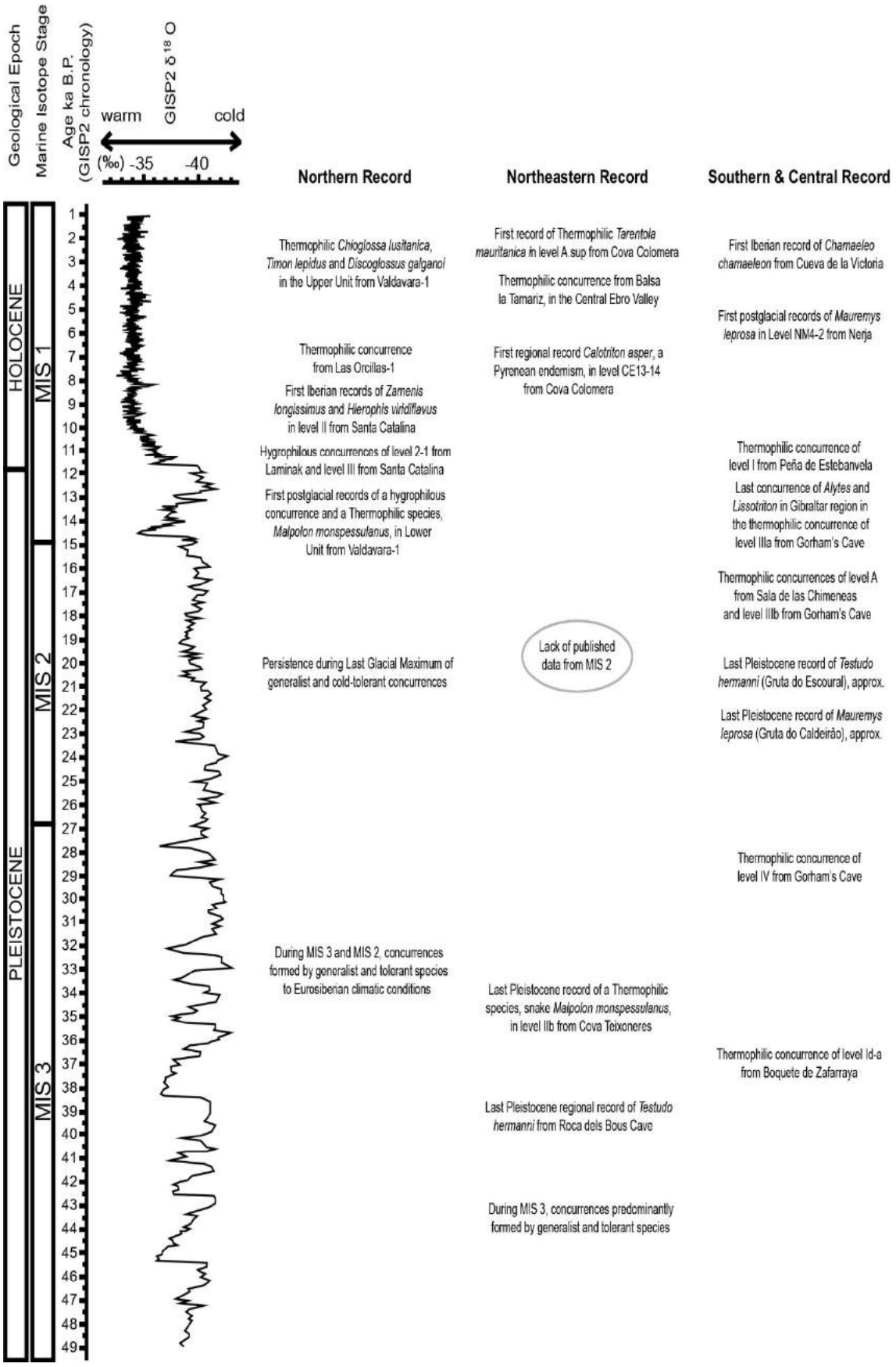

Figure 1.5.- Comparison of the main biogeographic changes and the most significant herpetofaunal assemblages in the Iberian Peninsula during the latest Quaternary with GISP2 oxygen isotope records (modified from Fletcher and Sánchez-Goñi, 2008).

without the total extinction of any species identified in the latest Pleistocene record (Figure 1.5). The appearance in the Holocene of species without an Iberian fossil record in the latest Pleistocene, such as the anuran *H. meridionalis*, the tortoise *Testudo graeca*, the gecko *H. turcicus* and the chameleon *C. chamaeleon*, has been linked to human introductions; all of them have clear phylogenetic relationships with populations located on the Maghrebian side of the Strait of Gibraltar (Pleguezuelos et al., 2008).

Z. longissimus is the only herpetofaunal case of a postglacial colonization from the other side of the Pyrenees currently verified both by the fossil record and by molecular studies (Musilová et al., 2010). However, this snake is unlikely to be the only taxon that used this route of colonization, as might have occurred with other reptiles with similar phylogeographies, such as *L. agilis* (Kalyabina et al., 2001) and *L. bilineata* (Brückner et al., 2001; Joger et al., 2001; Böhme et al., 2007), although there are no Iberian fossil records for these species. In the case of *H. viridiflavus*, which presents a postglacial fossil record in the Iberian Peninsula, the phylogeography of its Iberian populations is unknown (Nagy et al., 2002; Joger et al., 2007).

H. meridionalis, which is probably present in the Iberian Early Pleistocene (Blain, 2009; Agustí et al., 2010) but is apparently absent from the fossil record of the Late Pleistocene except for its appearance in the MIS 5b-a sequence of Vanguard's Cave (Gleed-Owen, 2001; Gleed-Owen and Price, 2011), has been reintroduced in recent times from two different areas of North Africa (Recuero et al., 2007). Something similar has been detected in the Iberian communities of *C. chamaeleon*, which were introduced from two populations in Atlantic and Mediterranean areas of the Maghreb (Paulo et al., 2002b).

H. turcicus could have colonized the thermophilic Iberian littoral from populations in North Africa (Carranza and Arnold, 2006; Mateo et al., 2011; Rato et al., 2011). Meanwhile, the two Iberian populations of *T. graeca* share haplotypes with Maghreb populations, having reached the Iberian Peninsula either by human introduction or by natural rafting from northern Algeria in rather recent times, adding to the modern contributions of Moroccan individuals in the Doñana area (Álvarez et al., 2000; Fritz et al., 2009; Graciá et al., 2011, 2013, Graciá and Giménez, 2015). These are generally species of anthropophilic tendencies and, in the specific cases of *T. graeca* and *C. chamaeleon*, cultural linkages and magical-religious practices are known that could have led to their intentional introduction by humans (Pleguezuelos et al., 2008).

Returning to the north of the Iberian Peninsula, the reptiles *L. bilineata*, *Z. longissimus* and *H. viridiflavus* would have crossed the Pyrenees during the postglacial stage. These three species have reduced distributions in the Iberian Peninsula, basically focused on the two ends of the Pyrenees, the Basque-Cantabrian and Catalan areas (Santos et al., 2002a, 2002b; Barbadillo, 2002). In contrast to their situation in Iberia, they have an extensive and widespread distribution in Mediterranean environments of the Italian Peninsula and Sicily (Gosá and Rubio, 2013). Their restricted distribution

in the Iberian Peninsula, despite their tolerance of fully Mediterranean climates and thermophilic environments, has been linked to competition with other Iberian species. *Z. scalaris* is considered the Iberian ecological equivalent of *Z. longissimus*, the two species excluding each other and appearing in sympatry only at the southern limit of the Pyrenean distribution of the latter species, but never in syntopy (Rubio and Gosá, 2010). Phenomena of allopatry by competition have been detected among *M. monspessulanus* and *H. viridiflavus* (Cortesogno, 1994; Naulleau, 1997), it being the competitive exclusion with *M. monspessulanus* that determines the southern boundary of the Iberian distribution of *H. viridiflavus* (Santos et al., 2010).

For *L. bilineata*, the existence of competitive exclusion with *L. schreiberi* and *T. lepidus* has also been suggested, though more data are needed to confirm this (Delibes and Salvador, 1986; Gosá and Rubio, 2013). *R. dalmatina*, which has a possible Pleistocene record in Erralla (Esteban and Sanchiz, 1985), could be included in the same category as the above-mentioned species on account of its reduced Iberian distribution range (Gosá, 2002), bounded to the south of the Basque Country and northern Navarra, in contrast to its expansion in Italy and the Balkans. This could be due to competitive exclusion processes with *R. temporaria* (Riis, 1997).

In projections of the current area of potential habitability for these four species in the Iberian Peninsula (Araújo et al., 2011), the potential viability of *R. dalmatina* is proposed along the Cantabrian fringe, in the northern half of Portugal and the western and central Pyrenees, where the potential area of *R. dalmatina* habitability overlaps with the distribution of *R. temporaria*. The same area of potential habitability is attributed to *L. bilineata*, where one of its possible Iberian ecological opponents is also located, the northwestern Iberian endemism *L. schreiberi*. For this latter lizard an area of potential habitability is proposed that ranges from the Basque Country to Catalonia through the Pyrenees and the southern pre-Pyrenean valleys, the two ends of the Pyrenees being occupied by *L. bilineata*. This reinforces the hypothesis of competitive exclusion between the two species of the genus *Lacerta*. By contrast, *Z. longissimus* and *H. viridiflavus*, which share roughly the same potential habitability area as *L. bilineata* and *R. dalmatina*, only come into direct conflict with *Z. scalaris* and *M. monspessulanus* in the Atlantic fringe that runs from the southern half of Galicia to the Tagus river.

However, it should be noted that Araújo et al. (2011) only include climate data for the Iberian populations in making their projections of potential distribution. Hence, it is possible that the potential habitability of *L. bilineata*, *Z. longissimus* and *H. viridiflavus* in Iberian Mediterranean regions has been underestimated due to the apparent Euro-Siberian affinities of these species in Iberia, when in fact they are species capable of living in much warmer areas in the other southern European peninsulas. For this reason, the hypothesis cannot be ruled out that the southern limits of their distributions are due to direct competition with *T. lepidus*, *Z. scalaris* and *M. monspessulanus*, respectively.

1.5. Conclusions

In all 58 Iberian archaeo-palaeontological sites with a herpetofaunal presence from the latest Pleistocene to the Late Holocene a total of 47 different taxa have been identified at generic and specific level. These are grouped taxonomically into eight urodelans: *P. waltl*, *S. salamandra*, *T. pygmaeus*, *T. marmoratus*, *I. alpestris*, *C. asper*, *C. lusitanica* and *L. helveticus*; 12 anurans: *A. obstetricans*, *A. cisternasii*, *D. galganoi*, *P. cultripes*, *Bufo* gr. *B. bufo*, *E. calamita*, *R. temporaria*, *R. dalmatina*, *R. iberica*, *P. perezi*, *P. punctatus* and genus *Hyla*; three chelonians: *M. leprosa*, *E. orbicularis* and *T. hermanni*; one amphisbaenian: *B. cinereus-mariae*; one iguanian: *C. chamaeleon*; one gecko: *T. mauritanica*; one anguimorph: *A. fragilis*; two skinks: *C. bedriagai* and *C. striatus*; five lizards: *A. erythrurus*, *P. algirus*, *T. lepidus* and genera *Lacerta* and *Podarcis*; and 13 snakes: *N. maura*, *N. natrix* sensu lato, *C. austriaca*, *C. girondica*, *H. hippocrepis*, *Z. longissimus*, *Z. scalaris*, *H. viridiflavus*, *M. brevis*, *M. monspessulanus*, *V. aspis*, *V. seoanei* and *V. latastei*.

The fossil herpetofaunal assemblages allow us to establish two major biotic regions during the latest Pleistocene, albeit with ill-defined limits because of the current lack of a continuum of palaeo-archaeological sites with a herpetological record between the two groups. The first biotic region is formed by the center and south of the Iberian Peninsula, with *E. calamita*, *Bufo* gr. *B. bufo*, *T. lepidus*, *Z. scalaris* and, to a lesser extent, *P. waltl*, *P. cultripes*, *T. hermanni*, *M. monspessulanus* and *V. latastei* as the most representative species of the herpetofaunal record. The second major biotic region comprises the Atlantic-Cantabrian facade and northeastern Iberia and is characterized by the association of *R. temporaria* and *A. fragilis* as the dominant species of the prehistoric sequences, although in the northern area they are accompanied by *Bufo* gr. *B. bufo*, *E. calamita* and the genera *Alytes* and *Vipera* as the most representative taxa, while in the northeastern Iberian record they are accompanied by *A. obstetricans*, *E. calamita*, *Bufo* gr. *B. bufo*, *P. punctatus* and *C. girondica* as the dominant species.

The palaeoclimatic implications of these large associations indicate the maintenance of typically warm Mediterranean conditions in the central and southern regions, while the northern and northeastern areas present a generally cold and humid climatic regime dominated by wooded spaces and wet meadows. However, this scenario may be affected by the possible bias of a record with widely scattered sites in the south and center of the Iberian Peninsula, and the absence of published herpetofaunal assemblages for MIS 2 of the northeastern area. New discoveries and publications, which may fill the gaps in the different regional records, will confirm or challenge these observations.

The main biogeographic changes occur after the beginning of the postglacial phase, with the resulting climate improvement that produced the expansion of the thermophilic species towards the north of the Iberian Peninsula, possibly taking advantage of the existence of natural corridors such as the Ebro Valley or the Atlantic coast. In parallel, new European species entered via the Pyrenean margins having passed through southern France; their

expansions may have been halted in the north by the contemporaneous colonization of Iberian Mediterranean species from the south. The introduction of various Maghrebian species, possibly caused by humans and dated by genetic studies to relatively recent times, represents the most recent processes of emergence and expansion of new amphibians and reptiles in the Iberian Peninsula during the Middle-Late Holocene.

Supplementary data

Appendix 1. Supplementary Table 1.S1.- Data matrix of the northern region with herpetofaunal assemblages from the latest Pleistocene to the Late Holocene (pages 211-212).

Appendix 2. Supplementary Table 1.S2.- Data matrix of the north-eastern region with herpetofaunal assemblages from the latest Pleistocene to the Late Holocene (page 213).

Appendix 3. Supplementary Table 1.S3.- Data matrix of the central and southern regions with herpetofaunal assemblages from the latest Pleistocene to the Late Holocene (page 214).

Capítulo 2

Objetivos globales

Una vez realizada la síntesis comparativa del registro arqueo-herpetológico ibérico, desde el Musteriense tardío de las últimas comunidades neandertales hasta la Edad del Bronce, se abren nuevas perspectivas para el conocimiento de los anfibios y reptiles en contextos arqueológicos del Cuaternario final como objetivo general de esta tesis doctoral.

En este sentido, otras investigaciones han señalado que el impacto humano sobre el paisaje ha ido aumentando a lo largo del Holoceno, alterándolo y transformándolo según sus necesidades, especialmente a partir del Neolítico (López-Sáez et al., 2014; Revelles, 2017; Carracedo et al., 2018). Este proceso de antropización ambiental en alza se inició con el aumento de la sedentarización de los grupos de cazadores-recolectores y con la difusión de la agricultura y la ganadería. Posteriormente continuó con la progresión de la complejidad y de la jerarquización social que desembocó en el surgimiento de las primeras culturas urbanas. Así, una mayor atención al registro arqueoherpetológico de esta fase cronocultural permitirá conocer mejor cómo se adaptaron las diferentes especies de anfibios y reptiles a los cambios producidos en el paisaje antropizado y a los nuevos nichos ecológicos generados por la creciente influencia humana, incluso dentro de las propias áreas de uso humano (hábitat, productivas, rituales, funerarias), infiriendo, así la afección sobre la composición de la herpetofauna.

Por ello, se estudiarán restos de microvertebrados de la Cueva de El Mirador (Burgos), un yacimiento kárstico de la Sierra de Atapuerca con una potente secuencia holocénica, que abarca desde el Neolítico hasta el Bronce Medio (Vergès et al., 2016). Este sitio arqueológico ya ha aportado varios registros que muestran la evolución del impacto humano en la paisaje del pasado, tanto arqueobotánicos (Allué y Euba, 2008; Rodríguez et al., 2016; Expósito et al., 2017) como a través de los pequeños mamíferos (quirópteros, insectívoros y roedores) (Bañuls-Cardona et al., 2013, 2017a, 2017b). En este contexto, durante el año 2000 fueron recuperadas veinte pequeñas tafocenosis de microfauna vertebrada, formadas muy mayoritariamente por herpetofauna, provenientes de los niveles del Calcolítico y la Edad del Bronce (Vergès et al., 2002). Los datos preliminares permiten plantear la hipótesis de que se trata de acumulaciones coprocenóticas generadas por la depredación de un animal carnívoro, que fueron preservadas en la cueva gracias a las especiales condiciones interiores. En el siguiente capítulo de esta tesis doctoral (Capítulo 3) se realizará el estudio tafonómico de la mayor de las acumulaciones recuperadas (la tafocenosis MIR5-P22-n4), para corroborar o no su origen coprocenótico

y postular un posible depredador (Capítulo 3).

También se realizará un estudio comparativo de la composición faunística de las acumulaciones, tanto sincrónica como diacrónicamente, para inferir las diferencias de representación en los taxones identificados y sus causas (Capítulo 4). Asimismo, se pondrá énfasis en la probable influencia de la antropización del paisaje y su impacto en la herpetofauna representada. Además, a través de la comparación con el resto del registro fósil del norte de la Península ibérica, se contextualizarán las asociaciones de herpetofauna de El Mirador dentro de las dinámicas de cambio del Holoceno en esta región (Capítulo 5).

Otro de los objetivos de esta tesis tiene que ver con los impactos humanos del Holoceno sobre las comunidades de reptiles y anfibios de la Península Ibérica en relación a la introducción de nuevas especies. Los datos recopilados en el capítulo anterior señalan la posible relación entre la llegada de nuevos taxones de herpetofauna a la Península Ibérica y la acción de diferentes movimientos humanos provenientes del litoral meridional mediterráneo durante el Holoceno, singularmente desde el Magreb según los estudios moleculares. Por ello son de especial interés aquellos períodos en los que se intensificaron los contactos culturales y comerciales entre las diferentes regiones mediterráneas, desde el Neolítico hasta la llegada de colonos y comerciantes orientales en la Edad de Hierro, principalmente fenicios y griegos (Aubet, 2009). El establecimiento del dominio romano en la Península Ibérica incrementó todavía más los vínculos con otras zonas del Mediterráneo, convertido en un mar interior del Imperio Romano por el que fluía gran parte de su comercio interior (Terpstra, 2019). La caída de la organización estatal del Imperio Romano Occidental en el siglo V d.C. no supuso el cierre del comercio mediterráneo, que continuó también con la conquista islámica del siglo VIII y las posteriores conquistas feudales cristianas (Constable, 2010; Ferrer, 2012; Balard, 2015; Esch, 2018). Estudios anteriores ya han vinculado el comercio marítimo antiguo y movimientos de personas y mercancías a la posible introducción, intencionada o no, de herpetofauna y otros grupos de pequeños vertebrados terrestres entre diferentes regiones de la Cuenca Mediterránea (por ejemplo, Dobson, 1998; Corti et al., 1999; Libois et al., 2001; Michaux et al., 2003; Cosson et al., 2005; Kornilios et al., 2010; Masseti y Zuffi, 2011; Pinya y Carretero, 2011; Valenzuela et al., 2016), en un precedente histórico al problema global contemporáneo de las especies exóticas e invasoras.

Así, en esta tesis doctoral se estudiará la recientemente descubierta población de eslizón ocelado (*Chalcides ocellatus*) en la Serra del Molar (Alicante), una pequeña elevación montañosa situada entre las desembocaduras de los ríos Vinalopó y Segura, en el sur valenciano. La especie *C. ocellatus* es una escinco de amplia distribución casi circunmediterránea, que de manera natural abarca desde el Magreb hasta el Próximo Oriente, Anatolia y el Egeo, además de varias islas del Mediterráneo Central y Oriental. Los datos moleculares aportados durante los últimos años señalan que *C. ocellatus* ha sufrido una muy reciente y rápida dispersión, especialmente a lo largo del

litoral oriental mediterráneo y en las costas meridionales del Mar Rojo, y que se ha relacionado con translocaciones humanas y al comercio antiguo (Kornilios et al., 2010; Lavin y Papenfuss, 2012). La nueva población de la Serra del Molar supone su primera cita en la Península Ibérica y la hipótesis inicial de trabajo es que se trata de una introducción humana. Para identificar su procedencia se realizará un estudio molecular a partir de la toma de muestras orgánicas de individuos vivos. Los resultados filogenéticos y filogeográficos de las muestras secuenciadas se confrontarán con la revisión de los registros arqueológico, histórico y geomorfológico de la Serra del Molar y de su región circundante para plantear los escenarios más plausibles de la llegada de los eslizones ocelados a la zona (Capítulo 6).

A modo de resumen, los objetivos globales de esta tesis doctoral son:

1. Abrir nuevas perspectivas para el conocimiento de los anfibios y reptiles en contextos arqueológicos del Cuaternario final (Holoceno).
2. Conocer cómo se adaptaron las diferentes especies de anfibios y reptiles a los cambios producidos en el paisaje antropizado del Holoceno.
3. Con el estudio de restos de microvertebrados de la Cueva de El Mirador, ver cómo la influencia humana afectó al desarrollo de nuevos nichos ecológicos para la herpetofauna y a su composición en las propias áreas de actividad humana (hábitat, productivas, rituales, funerarias).
4. Estudiar la relación entre la llegada de nuevos taxones de herpetofauna a la Península Ibérica como consecuencia del impacto humano, a partir del estudio molecular y filogeográfico de la recién descubierta población de eslizón ocelado (*C. ocellatus*) en la Serra del Molar (Alicante).

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Chapter 2

Global objectives

Once the comparative synthesis of the Iberian archaeo-herpetological record has been completed, from the late Mousterian of the last Neanderthal communities to the Bronze Age, new perspectives are provided as the general objective of this doctoral thesis for the comprehension of the herpetological record in archaeological contexts of the Late Quaternary.

In this respect, previous studies have reported that the human impact on the landscape has been increasing throughout the Holocene, altering and transforming it according to its necessities, notably since the Neolithic (López-Sáez et al., 2014; Revelles, 2017; Carracedo et al., 2018). This process of increasing environmental anthropization began with the increase in sedentarization of hunter-gatherer groups and the spread of agriculture and livestock. It then continued with the progression of social complexity and hierarchization that culminated in the emergence of the first urban cultures. Thus, more attention to the archaeo-herpetological record of this chrono-cultural phase will allow us a better knowledge about how the amphibians and reptiles adapted to the changes produced in the anthropized landscape and to the new ecological niches generated by the increasing human influence, even within the areas of human use itself (habitat, productive, ritual, burial), thus inferring the effect on the herpetofaunal composition.

For this reason, microvertebrate remains from Cueva de El Mirador (Burgos) will be studied, a karstic site in the Sierra de Atapuerca with a potent Holocene sequence, ranging from the Neolithic to the Middle Bronze Age (Vergès et al., 2016). This archaeological site has already provided numerous records which show the evolution of human impact on the landscape in the past, both archaeo-botanical (Allué and Euba, 2008; Rodríguez et al., 2016; Expósito et al., 2017) and through small-mammals (bats, insectivores and rodents) (Bañuls-Cardona et al., 2013, 2017a, 2017b). During the year 2000, twenty small taphocenoses of vertebrate microfauna were recovered, formed mainly by herpetofauna, from the Chalcolithic and Bronze Age levels (Vergès et al., 2002). Preliminary data suggest that these are coprocenotic accumulations generated by the predation of a carnivorous animal, which were preserved in the cave thanks to the special internal conditions. In the next chapter of this doctoral thesis (Chapter 3), the taphonomic study of the largest of the recovered accumulations (taphocenosis MIR5-P22-n4) will be carried out, in order to corroborate or not its coprocenotic origin and to postulate a possible predator (Chapter 3).

A comparative study of the faunistic composition of the

accumulations will also be carried out to infer differences in representation in the taxa and their causes, both synchronously and diachronically (Chapter 4). The possible influence of landscape anthropization and its impact on the represented herpetofauna will also be studied. Furthermore, through a comparison with the rest of the fossil record of the northern Iberian Peninsula, the herpetofaunal associations from El Mirador pellets will be contextualized within the change dynamics of the Holocene in this region (Chapter 5).

Another objective of this doctoral thesis is to document the human impacts during the Holocene on the amphibian and reptile communities of the Iberian Peninsula concerning the introduction of new species. The data collected in the previous chapter suggest the possible connection between the arrival of new herpetofaunal taxa to the Iberian Peninsula and the action of distinct human movements from the southern Mediterranean coasts in the Holocene, singularly from the Maghreb according to molecular studies. Therefore, we are especially interested in those periods in which cultural and commercial contacts between the different Mediterranean regions intensified, from the Neolithic to the arrival of eastern settlers and traders in the Iron Age, mainly Phoenicians and Greeks (Aubet, 2009). The establishment of Roman rule in the Iberian Peninsula further increased the links with other areas of the Mediterranean, which became an inland sea of the Roman Empire and the main route of its internal trade (Terpstra, 2019).

The fall of the state organisation of the Western Roman Empire in the 5th century AD did not result in the closure of Mediterranean trade, which also continued with the Islamic conquest in the 8th century and the subsequent Christian feudal conquests (Constable, 2010; Ferrer, 2012; Balard, 2015; Esch, 2018). Previous studies have already connected ancient maritime trade and movements of people and goods to the possible introduction, intentional or not, of herpetofaunal and other small terrestrial vertebrates among different regions of the Mediterranean Basin (e.g., Dobson, 1998; Corti et al, 1999; Libois et al., 2001; Michaux et al., 2003; Cosson et al., 2005; Kornilios et al., 2010; Masseti and Zuffi, 2011; Pinya and Carretero, 2011; Valenzuela et al., 2016), as a historical precedent to the contemporary global problem of alien and invasive species.

Thus, this doctoral thesis will study the recently discovered population of the ocellated skink (*Chalcides ocellatus*) in the Serra del Molar (Alicante), a small mountainous area located between the mouths of the rivers Vinalopó and Segura, in southern Valencian Country. The species *C. ocellatus* is an almost circum-Mediterranean skink, which naturally extends from the Maghreb to the Near East, Anatolia and the Aegean region, as well as several islands in the Central and Eastern Mediterranean. Molecular data provided during recent years indicate that *C. ocellatus* has suffered a very recent and rapid dispersal, specially along the eastern Mediterranean coasts and the southern shores of the Red Sea, and that it has been associated with human translocations and ancient trade (Kornilios et al., 2010; Lavin and Papenfuss, 2012). The new population of the Serra del Molar represents its first record from the Iberian Peninsula and the human introduction is the initial

hypothesis. To identify its origin, a molecular study will be carried out through the collection of organic samples from living individuals. The phylogenetic and phylogeographic results of the sequenced samples will be compared with a review of the archaeological, historical and geomorphological records from the Serra del Molar and its surrounding region in order to propose the most plausible scenarios for the arrival of the ocellated skinks to the area (Chapter 6).

To summarize, the global objectives of this doctoral thesis are:

1. To open new perspectives for the knowledge of amphibians and reptiles in archaeological contexts of the Late Quaternary (Holocene).
2. To know how the different species of amphibians and reptiles adapted to the changes produced in the anthropized landscape during the Holocene.
3. Through the study of microvertebrate remains from El Mirador, determine how human influence affected the development of new ecological niches for the herpetofauna and its composition in the areas of human activity (habitat, productive, ritual, burial).
4. To study the relationship between the arrival of new herpetofaunal species to the Iberian Peninsula as a consequence of human impact, based on the molecular and phylogeographic study of the newly discovered population of the ocellated skink (*C. ocellatus*) in the Serra del Molar (Alicante).

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Chapter 3

Elucidating anuran accumulations: massive taphocenosis of tree frog *Hyla* from the Chalcolithic of El Mirador cave (Sierra de Atapuerca, Spain)

Abstract

Anurans, such as frogs and toads, are occasionally very abundant in archaeo-palaeontological sites and representing more than 80% of the remains. These accumulations have been linked mainly to human consumption in the European context, by the preferential selection of body parts and by the presence of burning, and to a lesser extent, cut marks (as in Chalain 3, Baume d'Ogens, Kutná Hora-Denemark). However, there are also records of accumulations attributed to natural catastrophic events (Bois-Roche). This research presents a taphocenosis of microvertebrates of reduced dimensions (7.8x2.7x2.4cm) containing 2,526 bones, from El Mirador cave of Atapuerca (Burgos, Spain) contemporaneous to an adjacent Chalcolithic burial (ca. 4,500 BP). The taxonomical study has identified at least 12 different taxa, which include one urodele, two anurans, seven squamates and two rodents. Tree frogs, *Hyla* gr. *Hyla arborea* (*Hyla molleri*), constitutes 84% of the assemblage. Quantitative and qualitative taphonomic analyses are focused on *Hyla* bones and show the presence of breakage and digestion marks associated with animal predation, albeit in low percentages and in light or moderate degrees. Due to its characteristics, El Mirador accumulation has been identified as a pellet accumulation produced by a medium-large owl (category 2). The nocturnal raptor hunted its preys during a wet period in spring, when the reproduction of the tree frogs occurs, showing a possible evidence of opportunistic predation on a seasonal resource. These findings help to understand the importance of anurans in the trophic chains of Prehistoric times, not only among human groups but also among non-human predators.

3.1. Introduction

Amphibians are one of the least studied groups in the Quaternary fossil record, due to the lack of specialists, in comparison to other groups as the small mammals. Nevertheless, the discoveries and publications of the last decades are beginning to increase our knowledge about them. Anurans (as frogs and toads) occasionally appear in large accumulations or taphocenoses that are formed exclusively or almost entirely by a single species (e.g., Bailon, 1997; Blain and Villa, 2006). The Early Pleistocene and Middle Pleistocene sequences of the Atapuerca sites (Burgos, Spain) are good examples, where some anuran species are abundant in certain levels. This is the case of the toad *Epidalea calamita* in Gran Dolina cave of Atapuerca, the record of which accounts for 70% of all amphibian individuals during the Early-Middle Pleistocene (Blain, 2005; Blain et al., 2008).

Kyselý (2008) proposes five hypotheses to explain anuran accumulations in archaeological records: 1) mortality during hibernation or

aestivation, 2) natural traps, 3) non-human predation, 4) human consumption, and 5) ritual human activities. Other documented causes are catastrophic mortality, such as floods (Cochard, 2004), as well as the ethological troglophily and trogloxeny of many species of European amphibians (Montori and Martínez-Silvestre, 2015).

Human consumption has generated a significant number of archaeological records in the European context, from the Mesolithic to the Chalcolithic periods, with historical and ethnographic records that extend to the present day (Bailon, 1997; Hüster, 2004; Chiquet, 2005; Kyselý, 2008). They are located within habitation sites, both in sedentary contexts, mainly towns as Seeberg Burgäschisee-Süd (Boessneck et al., 1963), Chalain 3 (Bailon, 1997), Arbon Bleiche (Hüster, 2004), and Kutná Hora-Denemark (Kyselý, 2008), or in temporary settlements of hunter-gatherer societies as Baume d'Ogens cave (Chiquet, 2005).

The sequence of El Mirador cave in Atapuerca, whose excavation is still ongoing, has yielded a large amount of microvertebrate bones (>100,000), although only the small mammal record has been published to date (López-García, 2008; Bañuls-Cardona et al., 2013, 2017a, 2017b). Twenty concentrated accumulations containing microfaunal remains with a significant abundance of herpetofauna were found in the levels from the Chalcolithic to the Bronze Ages (MIR5 and MIR4). To determine their origin, a taphonomic analysis was performed on the major accumulation (MIR5-P21-n4), identified as a small taphocenosis with a high number of remains (2,526), mostly belonging to anuran amphibians (84.91% of NME).

Additionally, this accumulation was compared with other taphocenoses from the Late Pleistocene level of Bois-Roche cave (Cochard, 1998, 2004), the Neolithic settlement of Chalain 3 (Bailon, 1997), and the Chalcolithic site of Kutná Hora-Denemark (Kyselý, 2008). These three sites have yielded some of the largest accumulations of anurans in the European archaeological context and provide a comparative context with which to infer new perspectives about amphibian taphonomy. The amphibian assemblage from the Neolithic level of El Harhoura 2, a karstic cave on the western Atlantic coast of Morocco, has also been included (Stoetzel et al., 2008, 2010, 2011, 2012).

Currently, there is a lack of actualistic references on amphibian taphonomy and herpetological taphonomy in general. The modern references about non-human predation are limited by the low number of anuran remains and pellets/accumulations or by the predator (mainly, the common barn owl *Tyto alba*) in the available literature (e.g., Pinto Llona and Andrews, 1999; Rey and Sanchiz, 2005; Denys et al., 2018). Despite this, they are included in the Discussion.

3.2. El Mirador cave

El Mirador cave (*Cueva de El Mirador*) is located on the slopes of the southern tip of the Sierra de Atapuerca, within the municipality of Ibeas de Juarros, as part of the Atapuerca karst system. It is located at 42º 20' 58" N and 03º 30' 33" W and it rises to 1,033 m.a.s.l.

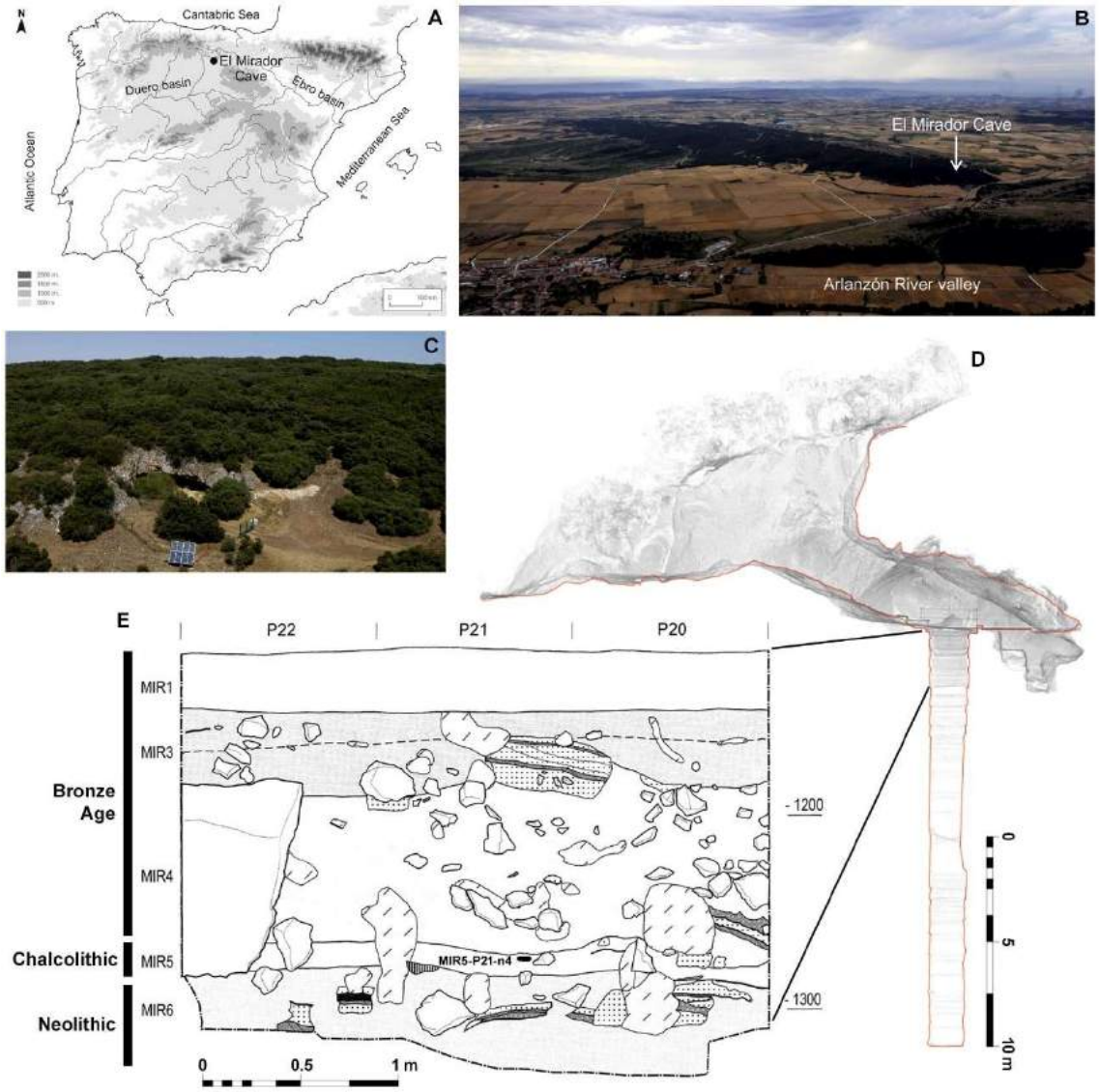

Figure 3.1.- El Mirador cave from Sierra de Atapuerca (Burgos, Spain). A: Location of El Mirador cave in the Iberian Peninsula; B-C: aerial views of El Mirador cave; D: N-S section of the cave with the test pit; E: stratigraphic profile from the Late Neolithic-Bronze Age south section of the test pit and the position of the MIR5-P21-n4 studied accumulation.

(Figure 3.1) over the middle basin of the Arlanzón River. The cave is currently 23 metres wide by 4 metres high and 15 metres deep, and is configured as an open shelter due to the collapse of the vault (Vergès et al., 2002).

Between 1999 and 2008, the archaeological work focused on a 6 m² test pit located in the central area of the western half of the cave, where a large Holocene succession was found, composed of 24 differentiated archaeological levels (Figure 3.1): Levels MIR1 and MIR2 are mixed layers formed by animal burrows and modern anthropogenic actions; MIR3 is partially disturbed, with mixed remains from the Middle to Late Bronze Age; MIR4 is a substantial level from the Middle Bronze

Age, which includes at its base a secondary burial of cannibalised human bones from the Early Bronze Age that were buried during the Middle Bronze Age (Cáceres et al., 2007; Vergès et al., 2016); MIR5 is a thin level with scarce anthropogenic contributions, but it is rich in small vertebrate remains (Vergès et al., 2002). The remaining Holocene levels (MIR6-24) are assigned to the Neolithic and are mostly made up of livestock pen waste, mainly *fumiers*, with the Late Neolithic represented in the top of the sequence (including MIR6) (Angelucci et al., 2009; Vergès et al., 2016).

MIR5 correspond to a phase of abandonment of the cave's use for livestock and represents a hiatus of one thousand years, between the Late Neolithic and the Bronze Age (Vergès et al., 2002), which possibly places it as contemporaneous with the Chalcolithic burial in MIR203 (4,880-4,390 cal. BP) (Ceperuelo et al., 2014, 2015; Lozano et al., 2015; Vergès et al., 2016).

3.3. Material and methods

3.3.1. *Sampling*

During the 2000 excavation campaign in El Mirador cave, a cylindrically shaped concentrated accumulation (7.8 cm in length, 2.7 cm in width and 2.4 cm in height) was identified containing sub-fossil microvertebrate remains on the roof of level MIR5 (z: 1284) and in grid P21 of the central test pit. This taphocenosis was isolated, its location was recorded, and it was removed. The bone remains were subsequently obtained in the Micropalaeontology laboratory of the Catalan Institute of Human Paleoecology and Social Evolution (IPHES) through screening with a running-water washing system and decreasing mesh sizes (5 mm, 2 mm and 0.5 mm).

3.3.2. *Taxonomic identification*

The following elements were used to identify the herpetofauna: postcranial skeleton for caudates (Gleed-Owen, 1998; Buckley and Sanchiz, 2012) and for anurans (Bailon, 1999; Blain and Arribas, 2017), skull bones and vertebrae for non-ophidian squamates (Anguidae, Scincidae, Lacertidae) (Barahona, 1996; Barahona and Barbadillo, 1997; Caputo, 2004; Blain, 2009), and vertebrae for snakes (Szyndlar, 1984). For the small mammals, the first lower molar for Arvicolinae and isolated teeth for *Apodemus sylvaticus* (Chaline, 1972; Cuenca-Bescós et al., 1997, 2008) were used.

The sexual determination of the anurans was based on the morphology of the humerus. The presence of a developed mesial crest in the distal part was used as a diagnostic character of the male sex, as opposed to its lower development in females (Bailon, 1999).

3.3.3. *Anatomical representation*

The minimum number of elements (MNE) was estimated from the total number of each element, specially the diaphysis. Among the fragmentary bones, the proximal-diaphysis-distal fragments were combined and counted as a single element. In the case of *Hyla* gr. *arborea*, the percentage of representation (PR) of each anatomical element was calculated according to that proposed by

Dodson and Wexlar (1979), which compares the observed quantity for each element versus the total expected amount:

$$PR = \frac{MNEi}{SAi \times MNI}$$

in which the minimum number of elements of each element (MNEi) is divided by the product of the multiplication of the specific amount (SAi) of each considered bone in a single individual by the minimum number of individuals (MNI) of *Hyla* gr. *arborea*.

Anatomical proportions were evaluated based on the following indices, adapted from Andrews (1990) and Cochard (1998):

- The index of representation of the postcranial skeleton in contrast to cranial skeleton:

$$\text{PC/C} = \frac{MNE[humeri\ +\ radioulnae\ +femora\ +\ tibiofibulae]}{MNE[the\ most\ represented\ cranial\ bone\ +\ angular]} \times \frac{4}{8} \times\ 100$$

  where *4/8* is the correction to compensate the difference in EA between the compared bones.

- The index of representation of the elements of the forelimbs in comparison with elements of the hindlimbs:

$$\text{FL/HL} = \frac{MNE[humeri\ +\ radioulnae]}{MNE[femora\ +\ tibiofibulae]} \times\ 100$$

- And the index of representation of the distal elements compared to the proximal elements of the extremities:

$$\text{D/P}\ = \frac{MNE[radioulnae + tibiofibulae]}{MNE[humeri + femora]} \times\ 100$$

3.3.4. *Digestion and breakage*

The taphonomic study is based on the methodology established by Andrews (1990) and adapted for amphibians by Pinto Llona and Andrews (1999), with contributions from Stoetzel et al. (2012) and Fernández-Jalvo and Andrews (2016), as well as the observations made on the studied sample (Figure 3.2). The degree of digestion has been classified into four grades (grade 0 - none, grade 1 - light, grade 2 - moderate, and grade 3 - heavy) based on the condition of the following modifications:

1) Rounding by the action of gastric acids on the sharp edges of the fractured bones before digestion. Initially it presents a slight smoothing over the fractures (1 - light), which as it increases, generates a greater rounding and polishing of the edges (2 - moderate) until the formation of very rounded and polished profiles (3 - heavy).

2) Cracking due to longitudinal fractures on the weakest parts of the bone element, mainly in the bone ends (1 - light), which can increase in length and width (2 - moderate) until it causes loss of the bone wall along the previous longitudinal lines (3 - heavy).

3) Thinning and plasticity of the bone walls, which to a greater degree can progressively produce a bowing towards the interior (1 - light), the collapse and the loss of sectors of the bone wall (2 - moderate) that extends through the bone as the digestion increases (3 - heavy).

4) Flaking by desquamation or exfoliation of the bone layers that can affect at surface level or the whole structure of the bone. Mostly this appears at the extremes of the bones or at the edges of the fractures, where small flakes are formed (1 - light), which at a more advanced stage increase the affected area and separate the different layers of the bone tissue (2 - moderate) and finally can

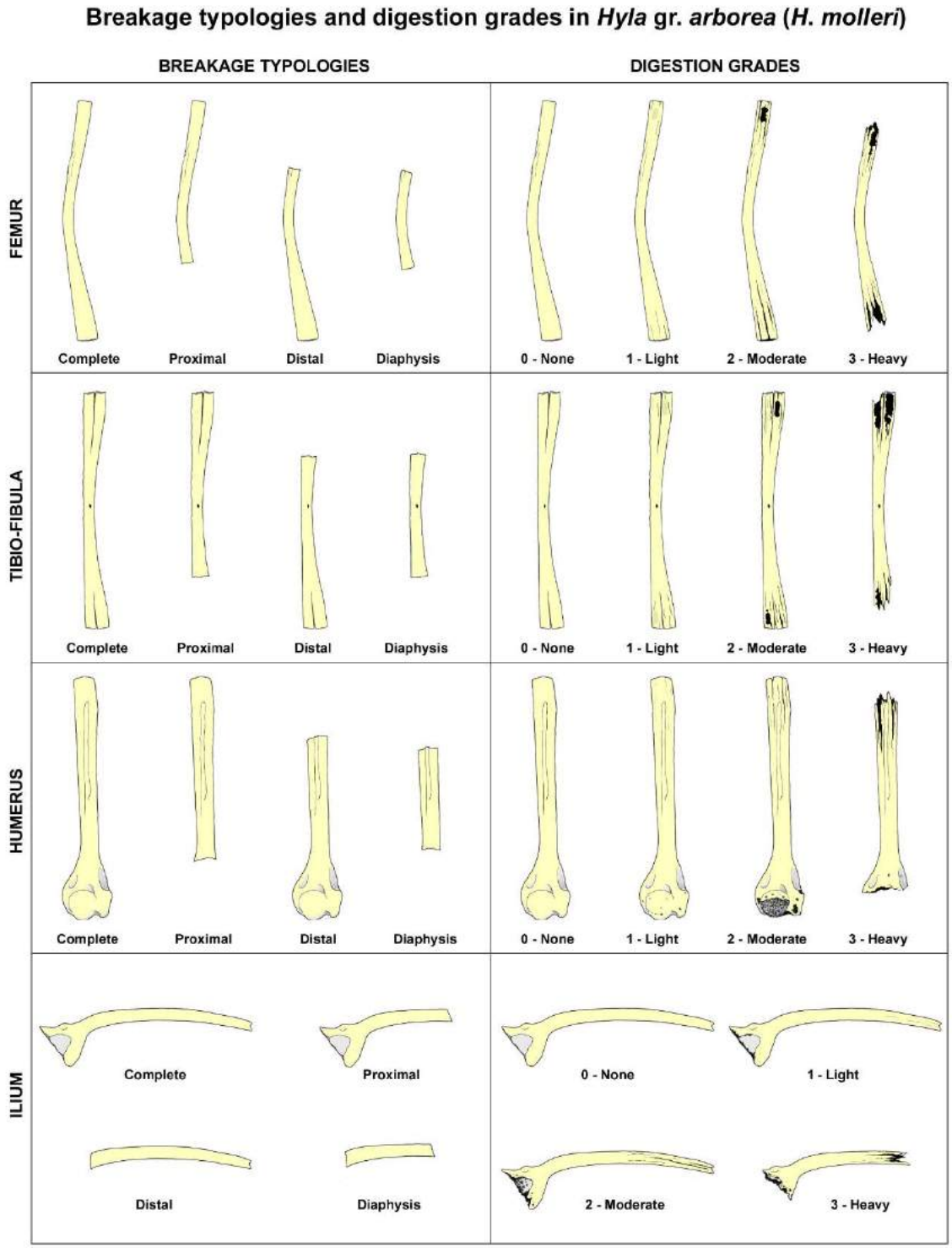

Figure 3.2.- Breakage typologies and digestion grades in *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave. The digestion grades represent the main digestive marks in the studied sample (splitting, thinning and bone collapse, and corrosion).

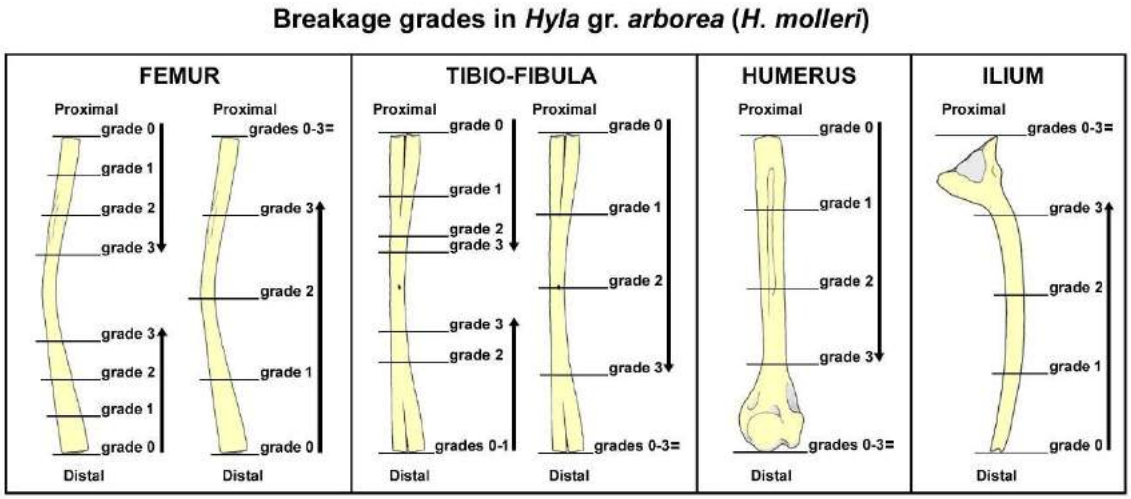

Figure 3.3.- Breakage grades in *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave. The arrows indicate the increasing breakage degree from one or both extreme parts (proximal and distal).

generate the loss of the outermost layers and the exposure of the internal tissues (3 - heavy).

5) Digestive corrosion that causes the progressive bone loss of the articular regions. In the first phase, small holes are produced in the more porous parts of the articular surfaces, primarily on the distal humerus and proximal ilium (1 - light). A higher degree of digestion increases the size of these holes and the internal cancellous tissue is exposed (2 - moderate), until most of the articular regions are lost due to corrosion (3 - heavy).

The different typologies of breakage refer to the conserved part of the element after the fracture associated to the predation: e.g., "proximal" means that the bone preserves the proximal part, including the diaphysis, but it has lost the distal part due to the breakage (Cochard, 1998). In Pinto Llona and Andrews (1999) have been established four grades to analyse the breakage, where grade 0 refers to any element that has conserved its proximal, diaphysis and distal parts, and grade 3 refers only to the preservation of the most compact part of the bone, with grades 1 and 2 in between but without a further description. In this article, grade 1 corresponds with the incipient loss on the parts, specially on the bone ends, up to 25% of its total length; and grade 2 corresponds to a comparatively greater but moderate loss, with the fracture of one or both parts, up to a maximum of 50% of the total length (Figure 3.3).

Both terminal articular epiphyses femur and tibio-fibula, and the proximal articular epiphysis of the humerus have not been included in the fracture analyses because of their porous tissue and weak structure, which may be affected by other conservation biases.

Microscope pictures were taken with the ESEM (environmental scanning electron microscope) at Rovira i Virgili University (URV), Tarragona.

3.4. Results

3.4.1. *Faunal list*

In total, 2,542 skeletal remains were registered in the taphocenosis MIR5-P21-n4, with a MNE of 2,035, which have been identified osteologically and assigned to the taxonomic level. They correspond to a MNI of 84, belonging to 12 different taxa, which include one urodele, two anurans, seven squamates and two rodents (Figures 3.4-3.5, Table 3.1; Appendix 4).

The predominant taxon is *Hyla* gr. *H. arborea*, with 1,706 remains belonging to a minimum of 66 individuals, corresponding to 83.83% of the identified MNE in the sample and 78.58% of the total MNI (Figure 3.5; Appendix 4). The sexual determination of the *H*. gr. *H. arborea* individuals, based on the morphology of the humerus, establishes the presence of a MNI of 34 males and 25 females over a total MNI of 66. This shows a prevalence of males versus females in a ratio of 1.36:1, but no significative difference.

3.4.2. *Hyla gr. H. arborea, skeletal representation*

Of the taxa in the accumulation, the *H*. gr. *H. arborea* remains can be studied in the most detail. All the bones of this species have been documented, except the vomer, squamosal, frontal-parietal, supra-scapula, cleithrum and sternum (Table 3.2). These absences can be attributed to differential preservation, due both to their small size and delicate configuration, and to the partial or total cartilaginous composition of some of these bones, which do not undergo advanced ossification, thereby limiting their preservation. A similar problem has occurred with the metapodials and phalanges, since conservation and identification biases cannot be ruled out due to their fragility and small size. Because of this they have not been included in the representation analyses.

At the quantitative level, the most represented elements (PR>80%) are the bones of the limbs (tibio-fibula, femur, and humerus), the pelvic girdle (ilium), shoulder girdle (scapula), and the vertebral region (dorsal vertebrae, sacral vertebra, and urostyle). In contrast, the most underrepresented elements (PR<10%) are the clavicle, the maxilla and the pterygoid (Table 3.2).

These three bones share a delicate configuration, with thin walls in contrast to the better-preserved elements, which are more massive and robust, again, possibly suggesting the occurrence of differential preservation in detriment to the more delicate elements.

According to the indices of anatomical representation (Table 3.3), proportionally there are twice as many postcranial bones than cranial elements in El Mirador accumulation. The distal long bones and proximal long bones are equally represented at the quantitative level, but there are fewer bones of the forelimbs than hindlimbs (82.47%).

Order	Species	Common name	MNE	MNE%	MNI	MNI%
Caudata	*Triturus marmoratus*	Marbled newt	36	1.77	3	3.57
Anura	*Hyla* gr. *H. arborea* (Hyla *molleri*)	(Iberian) tree frog	1,706	83.83	66	78.58
	Rana temporaria	European common frog	22	1.08	1	1.19
Squamata	*Anguis fragilis*	Slow-worm	12	0.59	1	1.19
	Chalcides striatus	Western three-toed skink	2	0.10	1	1.19
	Lacertidae indet. (small size)	Indeterminate small lizard	24	1.18	1	1.19
	Lacerta cf. *bilineata*	Western green lizard	93	4.57	3	3.57
	Timon cf. *lepidus*	Ocellated lizard	2	0.10	1	1.19
	Coronella austriaca	Smooth snake	110	5.41	2	2.38
	Vipera sp. (Vipera *aspis/seoanei*)	Viper	3	0.15	1	1.19
Rodentia	Rodentia indet.	Rodent	16	0.79	-	-
	Arvicolinae indet.	Vole	8	0.39	3	3.57
	Apodemus cf. *sylvaticus*	European wood mouse	1	0.05	1	1.19
Total			2,035	100%	84	100%

Table 3.1.-Taxonomic attribution, minimum number of identified elements (MNE), and minimum number of individuals (MNI) of the taphocenosis MIR5-P21-n4 from El Mirador cave (Atapuerca, Spain).

Anatomical parts and bones	MNE	SA	Expected	PR
Skull bones				**29.11%**
Premaxilla	11	2	132	8.33%
Maxilla	48	2	132	36.36%
Sphenethmoid	25	1	66	37.88%
Parasphenoid	19	1	66	28.79%
Pterygoid	12	2	132	9.09%
Prootic-exoccipital	92	2	132	69.70%
Angular	18	2	132	13.64%
Vertebrae				**76.55%**
Atlas	39	1	66	59.09%
Dorsal vertebrae	389	7	462	84.20%
Sacral vertebra	57	1	66	86.36%
Urostyle	53	1	66	**80.30%**
Shoulder girdle				**38.64%**
Clavicle	8	2	132	6.06%
Coracoid	38	2	132	28.79%
Scapula	107	2	132	81.06%
Forelimb				**78.41%**
Humerus	114	2	132	86.36%
Radio-ulna	93	2	132	70.45%
Pelvic girdle				**62.50%**
Ischium-pubis	20	1	66	30.30%
Ilium	125	2	132	94.70%
Hindlimb				**95.07%**
Femur	120	2	132	90.91%
Tibio-fibula	131	2	132	99.24%
Tarsus	187	4	264	**70.83%**
TOTAL	**1,706**		**2,838**	**60.11%**

Table 3.2.- Quantification of the minimum number of elements (MNE), the specific amount (SA) of each bone in a single individual, the expected number of elements from the total representation according to the minimum number of individuals (MNI = 66), and the percentage of presentation (PR), at the level of each bone and anatomic regions, in *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave.

	MIR5-P21-n4	B-R	CH3 VI ZA	CH3 VI ZB	KH-D F.36
Post-cranial vs. cranial	208.18%	158.97%	175.40%	4,496.67%	4,570%
Distal vs. proximal	95.73%	123.67%	60.07%	87.62%	167.25%
Forelimbs vs. hindlimbs	82.47%	69.47%	89.04%	19.49%	8.04%

Table 3.3.- Percentage values of the anatomic representation indexes: postcranial elements (humerus, radio-ulna, femur and tibio-fibula) versus cranial elements (most represented element plus angular), distal long bones (radio-ulna and tibio-fibula) versus the proximal long bones (humerus and femur), and of the anterior long bones (humerus and radio-ulna) versus the long posterior bones (femur and tibio-fibula) in *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave (MIR5.4) compared with those obtained in *Pelodytes punctatus* from Bois-Roche (B-R, Cochard, 1998), in *Rana temporaria* from Chalain 3 n.VI ZA. and Chalain 3 n.VI ZB (CH3 VI ZA and CH3 VI ZB., Bailon, 1997) and in *Rana temporaria* from Kutná Hora-Denemark F.36 (KH-D F.36, Kyselý, 2008).

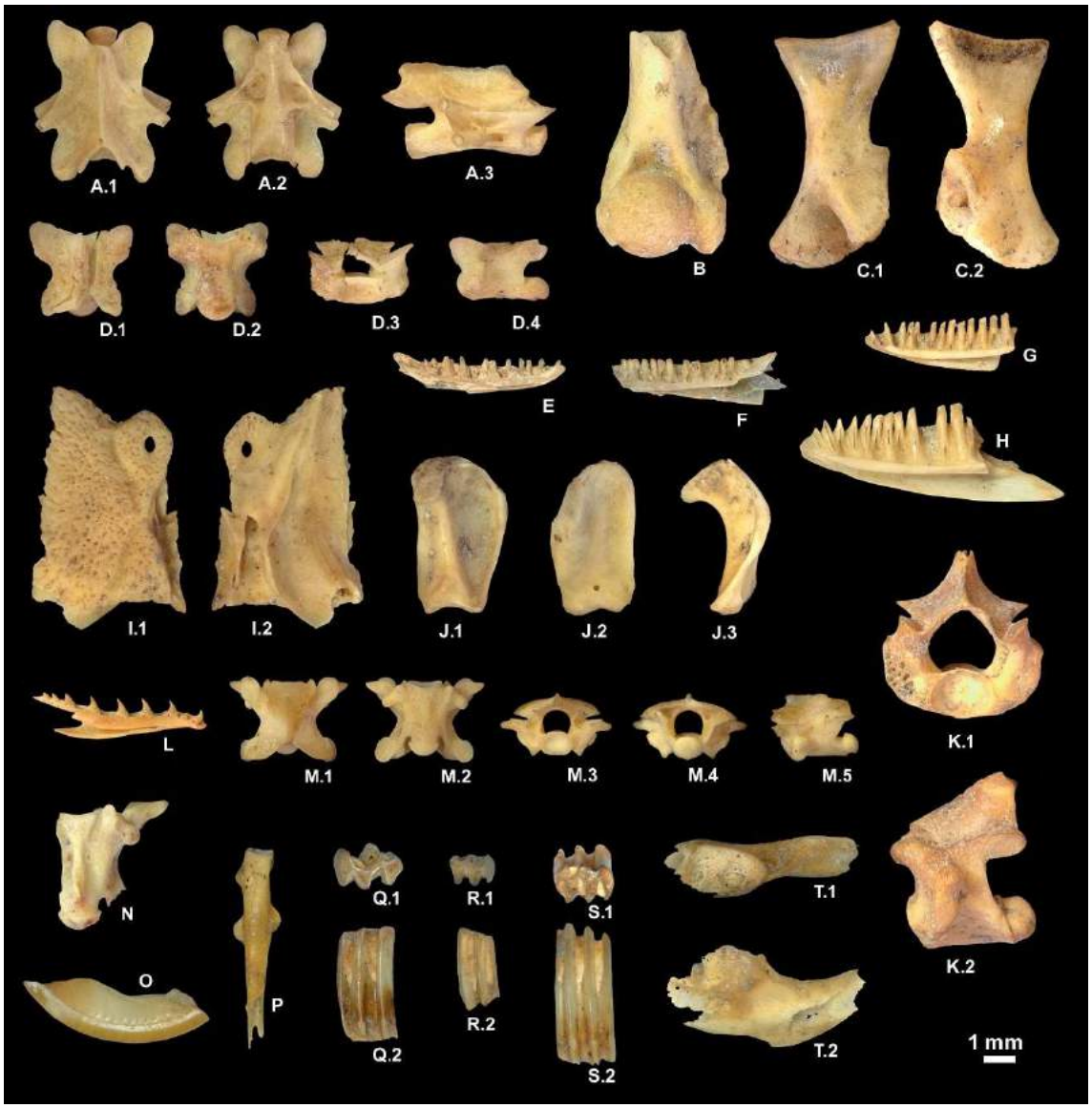

Figure 3.4.- Small vertebrates of the taphocenosis MIR5-P21-n4 from El Mirador cave. **A**: *Triturus marmoratus*, trunk vertebra, dorsal (A.1), ventral (A.2) and right lateral (A.3) views; **B-C**: *Rana temporaria*, **B**: right humerus, ventral view, **C**: right scapula, ventral (C.1) and dorsal (C.2) views; **D**: *Anguis fragilis*, trunk vertebra, dorsal (D.1), ventral (D.2), left lateral (D.3) and anterior (D.4) views; **E-F**: *Chalcides striatus*, **E**: left dentary, medial view; **F**: right dentary, medial view; **G**: Lacertidae indet. (small size), right dentary, medial view; **H-J**: *Lacerta* cf. *bilineata*, **H**: right dentary, medial view; **I**: parietal, dorsal (I.1) and ventral (I.2) views; **J**: quadrate, anterodorsal (J.1), posterodorsal (J.2) and lateral (J.3) views; **K**: *Timon* cf. *lepidus*, cervical vertebra, anterior (K.1) and left lateral (K.2) views; **L-M**: *Coronella austriaca*, **L**: left dentary, medial view; **M**: trunk vertebra, dorsal (M.1), ventral (M.2), anterior (M.3), posterior (M.4) and left lateral (M.5) views; **N**: *Vipera* sp., trunk vertebra, ventral view; **O-P**: Rodentia indet., **O**: left upper incisive, labial view; **P**: left ulna, posterior view. **Q-S**: Arvicolinae indet., **Q**: right upper molar (M2), occlusal (Q.1) and labial (Q.2) views; **R**: left upper molar (M3), occlusal (R.1) and labial (R.2) views; **S**: right upper molar (M1), occlusal (S.1) and lingual (S.2) views; **T**: *Apodemus* cf. *sylvaticus*, right mandible, occlusal (T.1) and labial (T.2) views.

Figure 3.5.- *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave. **A**: left premaxilla, medial view; **B**: left maxilla, medial view; **C**: parasphenoid, ventral view; **D**: right pterygoid, dorsal view; **E**: right angular, dorsolateral view; **F**: atlas, anterior view; **G**: anterior trunk vertebra, dorsal (G.1) and anterior (G.2) views; **H**: posterior trunk vertebra, dorsal view; **J**: urostyle, dorsal view; **K**: right coracoid, dorsal view; **L**: right clavicle, dorsal view; **M**: left scapula, dorsal view; **N**: male right humerus, ventral view; **O**: left radio-ulna, ventral view; **P**: femur, lateral view; **Q**: tibio-fibula, ventral view; **R**: left tarsus with articular epiphyses, ventral view; **S**: isquion-pubis, posterior view; **T**: right ilium, lateral view.

3.4.3. *Hyla gr. H. arborea, breakage and digestion*

The percentage of breakage of the main long bones is low or very low in all analysed elements (Figure 3.6B-C; Figure 3.7). The femora exhibit less evidence of fracture losses, with a very high percentage of bones preserving their full length with marginal losses at the ends (Figure 3.6B). In contrast, the ilia are the most affected bones, with almost all fractures concentrated in the loss of the anterior projection (25.6%), and a low percentage of breakage loss in the articular area of the acetabulum (1.6%), the most compact part of the bone.

The humeri and the tibio-fibulae have similar percentages of loss on their proximal extremes (11.45-12.28%). They differ in the low percentage of fracture at the distal end of the humeri (5.26%), which involves the loss of the condyle and the epicondyles, while the tibio-fibulae show a low percentage of fracture loss on both extremes, only preserving the diaphyses (6.11%) (Figure 3.7).

The most affected element by digestion is again the ilium, with 46.6% bearing gastric alterations, while the least affected is the tibio-fibula (15.27%) (Figure 3.7). The main alterations consist of longitudinal splits along the anterior projection and, to a lesser extent, corrosions in the area of the acetabulum and in the joint region with the ischium-pubis (Figure 3.6G). In the humeri, corrosions appear mainly in the condyle area, where the bone is more porous and permeable to the action of stomach acids during digestion (Figure 3.6H-I). The longitudinal splits are circumscribed mainly to the proximal half of the humerus diaphysis. Digestion marks are concentrated in the long bones of the hindlimb at its distal and proximal ends. Long splits appear in the femora and tibio-fibulae, as does loss of bone mass due to thinning, in the heavier cases with partial inwards curving and collapse (Figure 3.6D-F). This type of gastric alteration is absent in the humeri and ilia, possibly due to the different configuration of these bones, which are more porous and internally compact in their joint areas.

In general, the coincidence of two different digestion marks in a single element is rare, and mainly consists of splitting with gastric corrosion in ilia (1.6%) and humeri (5.26%) and splitting with thinning in femora (0.83%) and tibio-fibulae (0.76%) (Figure 3.6E). Only tibio-fibula displays rounding on the fracture edges (0.76%) which have been identified and associated with digestion (Figure 3.6C). Another taphonomic agent not associated with predation that has been documented is the possible action of roots on one femur, causing grooves over the external surface and a small perforation (Figure 3.6A).

According to the criteria established by Pinto Llona and Andrews (1999) on anurans remains, the MIR5 assemblage corresponds to a breakage category 2, because most of the bones are complete, and a digestion category 2, because the effects of digestion are relatively low in degree and percentage (Table 4, Figure 3.7).

3.4.4. *Taphonomy of the remaining taxa*

The bones of the other taxa represented in the accumulation exhibit a low percentage of breakage and/or digestion. The high degree of breakage of

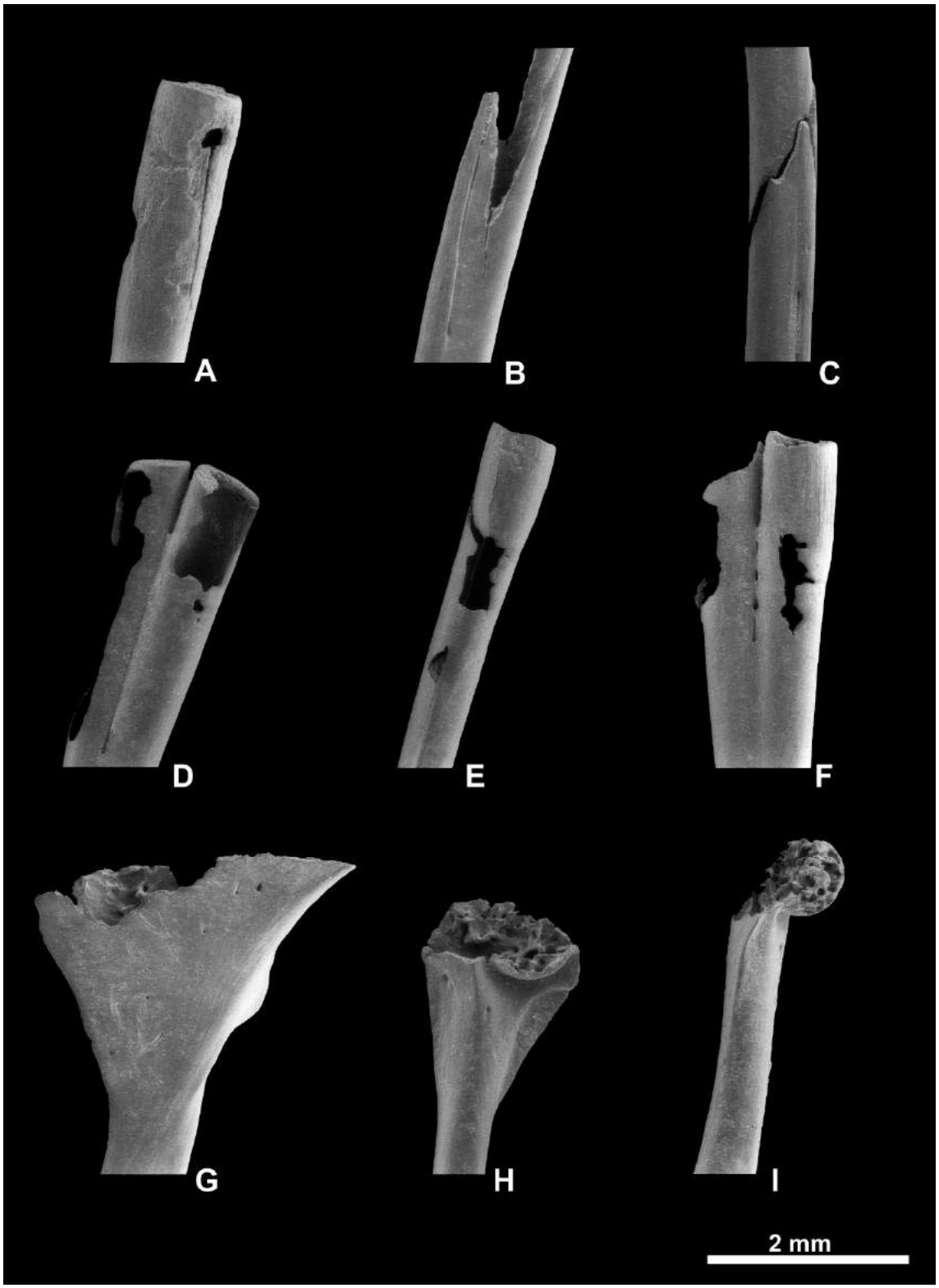

Figure 3.6.- Taphonomic marks on *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave: A) marks of roots on proximal femur; B) fractures on proximal femur; C) light rounding on fracture edges on the diaphysis of tibio-fibula; D) Moderate thinning and bone collapse on distal tibio-fibula; E) moderate thinning and bone collapse and light splitting lines on proximal femur; F) thinning, bone collapse and splitting lines on distal tibio-fibula; G) moderate corrosion on proximal ilium; H) and I) moderate corrosions on distal humeri.

the larger elements stands out, such as the dentaries, frontals and parietals of the lizards (*Lacerta* cf. *bilineata* and *Timon* cf. *lepidus*) (Figures 3.3H, 3.3I), and the tibio-fibulae and humeri of *Rana temporaria* (Figure 3.4B). However, other smaller elements are mostly intact, such as the vertebrae of *Coronella austriaca* and *Triturus marmoratus* (Figures 3.3A, 3.3M). The strongest evidence of digestion is visible in the dorsal vertebrae of *Anguis fragilis*, with cracks following lines of weakness (Figure 3.4D.1); in the vertebra of *Timon* cf. *lepidus*, with partial loss due to corrosion in the right synapophysis and neural spine (Figure 3.4K.1); as well as in the proximal region of the right scapula of *R. temporaria* (Figure 3.4C.1). Another digestion alteration is the rounding of the fracture edge in the diaphysis of the right humerus of *R. temporaria* (Figure 3.4A).

Among the small-mammal remains, two Arvicolinae molars show evidence of digestion in the form of dissolution on the enamel edges: one with a light degree (Figure 3.4Q) and the other with a moderate degree (Figure 3.4R). The mandible fragment assigned to cf. *Apodemus* cf. *sylvaticus* presents traces of heavier digestion with loss of the posterior part (Figure 3.4T). Other corrosion interpreted as light digestion were identified on a caudal vertebra, the scapula and on the proximal epiphysis of the ulna (Figure 3.4P).

3.5. Discussion

3.5.1. *Comparison with the archaeological record*

The comparison between the taphocenosis MIR5-P21-n4 from El Mirador cave, dominated quantitatively by *H.* gr. *arborea*, with other significant accumulations of anurans in the European archaeological record has allowed us to establish differences with regard to their origins (Table 3.5, Figure 3.8). The comparative analysis of PR for each element or anatomical group with those obtained in *P. punctatus* from Bois-Roche (Cochard, 1998, 2004), in *R. temporaria* from Chalain 3 n.VI (Bailon, 1997), and from Kutná Hora-Denemark F.36 (Kyselý, 2008) shows a similar pattern in the posterior part of the body of the anurans, with a very high PR for the hindlimbs (femora, tibio-fibulae), and partially for the ilia (Figure 3.8). The accumulation from El Mirador cave presents higher values, significantly in the skull elements, vertebrae, scapulae, radio-ulnae, femora, and tarsi. The lowest PR values occur in the ischia-pubis (30.30%) and coracoids (28.79%), although these are relatively high values compared to the rest of the record. El Mirador shares the general tendency of high PR values both in the ilia and in the bones of the hindlimbs, but differs from the other accumulations in the high PR of the forelimb bones (humeri and radio-ulnae) and scapulae.

These high percentages from El Mirador contrast with those exhibited in Chalain 3 n.VI ZB and Kutná Hora-Denemark F.36. Both accumulations present low PR in almost the entire skeleton, except in the urostyle (9.80-26.71%), humerus (13.80-33.06%) and ilium (26-29.32%), but primarily in the femur (57.70-84.04%) and tibio-fibula (99.84-100%). In contrast, Chalain 3 n.VI ZA presents a high PR of the urostyle (98.04%) and ilium (100%), but lower percentages for femur (68.45%), and significantly lower for tibio-fibula

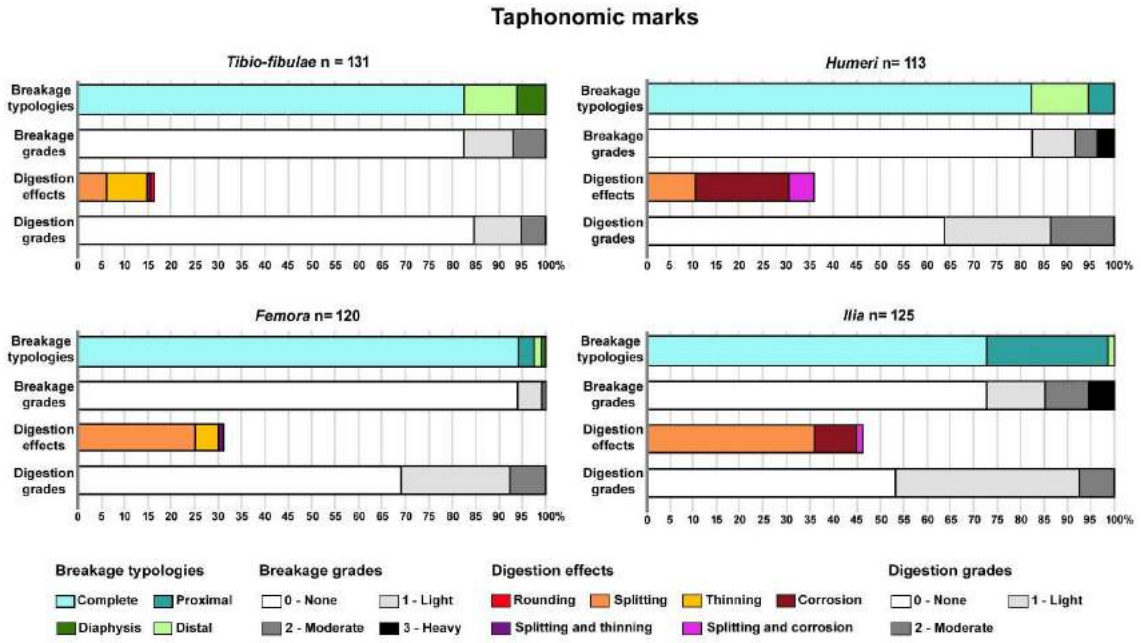

Figure 3.7.- Distribution and grades of the breakage, and effects and grades of digestion in the main long bones (humerus, femur, tibio-fibula and ilium) of *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave.

(65.69%). The Bois-Roche accumulation presents more moderate PR values, although it also has a substantial deviation towards higher PR values for the ilia and the hindlimbs. The predominance of the long bones of the hindlimbs versus the long bones of the forelimbs was observed in all accumulations, notably in Chalain 3 n.VI ZB and Kutná Hora-Denemark F.36 (19.49% and 8.04%, respectively), which also have an enormous predominance of postcranial elements over cranial bones (4,496.67% and 4,570%) (Table 3.3).

The archaeological sites bearing evidence of human consumption of the frog *R. temporaria*, like Mesolithic Baume d'Ogens (Chiquet, 2005), Neolithic Chalain 3 (Bailon, 1997), and Chalcolithic Kutná Hora-Denemark (Kyselý, 2008), are characterised by the high representation of the hindlimbs and pelvic girdle compared to any other skeletal part. This preferential representation of the hind parts of the frogs' body is related to its greater meat supply. This bias is significant, taking into account the PRs, in the taphocenosis of the ZB area of Chalain 3 N.VI and of pit 36 from Kutná Hora-Denemark, with a very high representation of the tibio-fibula (ca. 100%), while in Baume d'Ogens, the ilium is the most represent-ted element in the accumulation. Similar representation patterns with predominance of the hindlimb bones of *R. temporaria* have also been identified in other sites, like in the Neolithic settlements of Motte-aux-Magnins from Clairvaux-les-Lacs (Jura, France) (Rage, 1989), Seeberg Burgäschisee-Süd (Solothurn, Switzerland) (Boessneck et

Percentage of breakage (%)	**Humeri n= 114**	**Ilia n= 125**	**Femora n= 120**	**Tibio-fibulae n= 131**
Grade 0 (Complete)	82.5	72.8	94.2	82.4
Grade 1	8.8	12.8	5.0	9.9
Grade 2	5.2	8.8	0.8	7.7
Grade 3	3.5	5.6	0	0
Total Breakage	17.5	27.2	5.8	17.6

Percentage of digestion (%)	**Humerus n= 114**	**Ilium n= 125**	**Femur n= 120**	**Tibio-fibulae n= 131**
Grade 0 - None	64.0	53.6	69.2	84.7
Grade 1 - Light	21.9	38.4	22.5	9.9
Grade 2 - Moderate	14.1	8.0	8.3	5.4
Grade 3 - Heavy	0	0	0	0
Total Digestion	36.0	46.4	30.8	15.3

Table 3.4.- Percentages according to grades of breakage and digestion in *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave.

al., 1963) and Arbon Bleiche (Thurgau, Switzerland) (Hüster, 2004).

Unlike in the ZB area, the accumulation of *R. temporaria* in the ZA area of Chalain 3 N.VI yielded PRs that are noticeably greater for the ilium, the urostyle and the humerus, which reach PRs very close or equal to 90-100%, and in general, greater PRs for the remaining bones that are underrepresented in the other area inside the site. According Bailon (1997) this has been explained by a functional difference between the two areas: ZA could have been the area where the frogs were processed, coinciding with the location of the central bonfire of the Neolithic cabin, while in ZB the cooked or consumed remains could have been redistributed.

Further evidence of human consumption is the presence of burning, which in Baume d'Ogens is seen on 59% of the bones, mainly affecting the ilia, which are burned in 73.27% of cases (Chiquet, 2005). The action of fire on anuran remains has been documented in Chalain 3, affecting 4.7% of the sample (Bailon, 1997), and 10.2% of the sample from pit 36 of Kutná Hora-Denemark (Kyselý, 2008). Also, the presence of cut marks on three bones (on a radio-ulna, tibio-fibula and coracoid) of *R. temporaria* from Arbon Bleiche has been identified as evidence of processing for human consumption (Hüster, 2004). Remarkably, this site also yielded remains of the endoparasitic nematode *Dioctophyma* in human faeces, an organism that uses anurans as transitory hosts during its lifecycle (Le Bailly and Bouchet, 2004). Further coprological evidence of the human consumption of frogs comes from level VI of Chalain 3, where human excrement was found to contain 59 remains of *R. temporaria*. Remains of this species were also found in seven dog coprolites. In all cases the

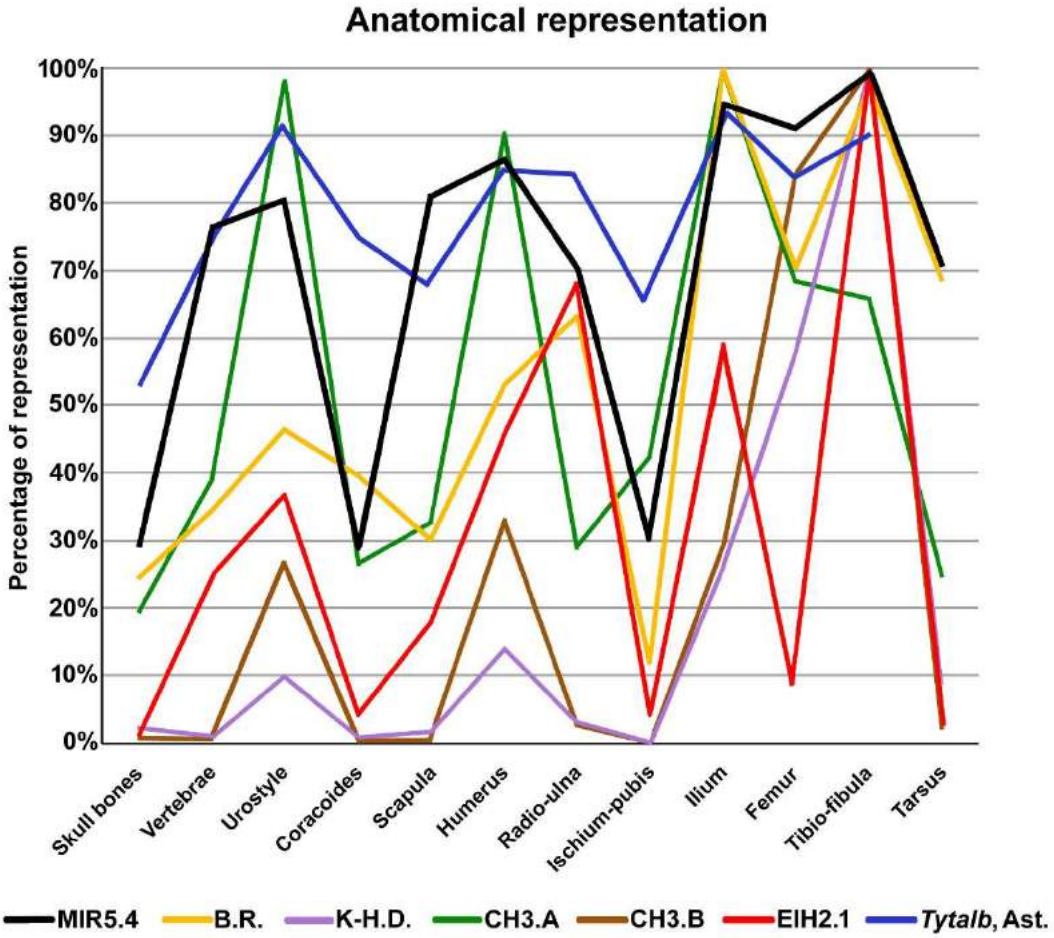

Figure 3.8.- Comparison between the percentages of representation (PR) of each bone element in *Hyla* gr. *H. arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave (MIR5.4) compared with those obtained in *Pelodytes punctatus* from Bois-Roche (B.R., Cochard, 1998), in *Rana temporaria* from Chalain 3 n.VI ZA. and Chalain 3 n.VI ZB (CH3.A and CH3.B., Bailon, 1997), in *Rana temporaria* from Kutná Hora-Denemark F.36 (K-H.-D., Kyselý, 2008), in the anuran accumulation from Level 1 of El Harhoura 2 (ElH2.1, Stoetzel et al., 2012) and from modern *Tyto alba* accumulation from Asturias, Spain (*Tytalb*, Ast., Rey and Sanchiz, 2005).

anuran bones presented very high breakage and extreme digestion modifications (Bailon, 1997).

These characteristics associated with human consumption, mainly the preferential selection of anatomical parts and the evidence of thermal alterations by the action of fire or cut marks, have not been found in El Mirador. Moreover, the tree frog *Hyla* is very small and therefore provides very little meat compared to edible frogs, which in Europe belong to the Ranidae family (Mattison, 2011).

The accumulation of a large number of *P. punctatus* (MNI = 176) in level 1a from the latest Pleistocene of Bois-Roche cave (Charente, France) has been associated with a catastrophic mortality caused by flash floods in the cave during the period of hibernation or estivation of the anurans inside it (Cochard, 1998, 2004). The remains of *P. punctatus* were distributed in several

small taphocenoses across the horizontal plane of the level, preserving all elements of the skeleton and, in general, had a comparatively high PR of 52.3% of the total. Breakage in the Bois-Roche sample affects 79.7% of the remains, but no evidence of digestion has been identified, so the high fracture percentage has been linked to a conservation factor during sedimentation or after it, without significant negative impact from other abiotic agents (Cochard, 2004).

The sex and age determinations in Bois-Roche point to a majority of females (>65%) compared to males (<15%), as well as to the existence of immature juveniles (<20%). This suggests that the catastrophic mortality event took place at the beginning of spring, as immature individuals and males of *P. punctatus* abandon the winter shelters before the females (Cochard, 2004). This demographic sample from Bois-Roche contrasts with Chalain 3 and Kutná Hora-Denemark, which show very marked biases in favour of males: in level VI of Chalain 3 the male frogs represented 70% of the individuals (Bailon, 1997), while in pit 36 of Kutná Hora-Denemark the percentage of males climbs up to 94.12% (Kyselý, 2008). In Baume d'Ogens, of a total 96 MNI, only the presence of 18 MNI-male could be sexed compared to 10 MNI-female (Chiquet, 2005). Bailon (1997) and Kyselý (2008) link the high representation of males and adult individuals in the accumulations with a systematic (for Kyselý) or opportunistic (for Bailon) hunting strategy of *R. temporaria* for human consumption during its reproduction period, between February/March to April, when the males are concentrated in ponds waiting to attract the females with sonorous calls.

3.5.2. *Coprocenotic scenario, a natural history*

The recovery of very compact cylindrical or oval-shaped accumulations of microvertebrate remains and the presence of multiple taphonomic alterations associated with non-human animal predation, such as digestive corrosion effects, during the fieldwork at El Mirador are concordant with a coprocenotic origin. The thinning and collapse of the bone walls and the low degree of rounding at the edges of the fractures, together with the relatively low degree of gastric alterations, rules out any carnivorous mammal as their source and suggests an avian raptor as the accumulation producer (Pinto Llona and Andrews, 1999).

The absence or presence of anthropogenic marks cannot be used to directly determine the human or non-human origin of the accumulation. The anuran and squamate remains from El Harhoura 2 cave (Morocco) show the continuous presence of burning throughout its sequence, reaching up to 9% of the total elements in Level 1, dated to the Neolithic (5800 BP, Stoetzel et al., 2012). But the presence of burnt anuran bones in El Harhoura 2 is not related to a specific pattern of burning or cut marks but rather they appear at an ashen layer, so they have been interpreted as post-depositional effects and probably accidentally burnt (Stoetzel et al., 2011, 2012). In the Neolithic level 1, one radio-ulna of *Bufo* s.l. have been found with traces looking like anthropic cut marks (ten parallel but irregular striations), which have been identified as possible evidence of marginal human consumption of toads during the Neolithic period, although most of the

Site	El Mirador	El Harhoura 2	Bois-Roche	Chalain 3	Kutná Hora-Denemark
Typology	Cave	Cave	Cave	Open air settlement	Open air settlement
Level	MIR5	1	1a	N.VI	F.36
Dimensions (taphocenosis)	Concentrated in a massive accumulation of 7.8x2.7x2.4 cm	Dispersed in 25 m^2, thickness 20-180 cm	Concentrated in 1 m^2, thickness 10-12 cm	Dispersed in 84 m^2, thickness 5 cm	Dispersed inside a pit of 1.4x1.2x0.25 m
Chronology	Chalcolithic	Neolithic	Late Pleistocene (MIS5-4)	Neolithic	Chalcolithic
Dominant species (%NMI)	*Hyla* gr. H. *arborea* (*Hyla molleri*) 84% (66 NMI)	*Bufo* s.l. (*Bufo spinosus* and *Sclerophrys mauritanica*) 64% (11 NMI)	*Pelodytes punctatus* 89% (174 NMI)	*Rana temporaria* 99% (868 NMI)	*Rana temporaria* 100% (123 NMI)
Breakage	Yes	Yes	Yes	Yes	Yes
Digestion	Yes	Yes	No	Yes	No
Burning	No	Yes	No	Yes	Yes
Cut marks	No	Yes	No	Yes	No
Other marks or evidences	Post-depositional alterations (root marks)	Post-depositional alterations (root marks, black traces, coating, burning, corrosion, rounding weathering, trampling)	Post-depositional alterations (fragmentation)	Human and dog coprolites	Post-depositional alterations (possible trampling)
Hypothesis	Owl predation, pellet	Owl predation, possible marginal human consumption	Catastrophic mortality	Human consumption, marginal canine consumption	Human consumption
References	This study	Stoetzel et al., 2008, 2010, 2011, 2012	Cochard, 1998, 2004; Blain and Villa, 2006	Bailon, 1997	Kyselý, 2008

Table 3.5.- Characteristics of the main accumulations of anurans in archaeological contexts from Late Quaternary in Western Palearctic.

characteristics associated with human consumption are missing (preferential selection of body parts, chewing marks, intentional burns, more flesh marks) (Stoetzel et al., 2012). A category 1-2 predator has been postulated as the main accumulator of anuran remains in El Harhoura 2, possibly a medium-sized owl such as *Bubo ascaphalus* (Stoetzel et al., 2012).

The PR in anurans from Level 1 of El Harhoura 2 shows a low representation of most elements in comparison with El Mirador accumulation, with the highest values in tibio-fibulae (100%), radio-ulnae (68.2%) and ilia (59.1%), and highlights the very low representation of femora (9.1%) (Stoetzel et al., 2012). The low total PR of this assemblage (27.4%) is possibly

because it is material dispersed over an extensive archaeological level (25 m^2) (Stoetzel et al., 2008, 2010, 2011, 2012) (Figure 3.8). The presence of 140 anuran individuals (117 *Discoglossus galganoi*, 20 *R. temporaria* and 3 *Hyla molleri*) was documented in a large contemporary accumulation generated by *T. alba* from Asturias, northern Spain (Rey and Sanchiz, 2005). The total PR is very high (78.9%), in accordance with that was assigned to *T. alba* (e.g., Andrews, 1990; Pinto Llona and Andrews, 1999), with the lowest value of the assemblage for the cranial bones (53.9%), and the highest values for the ilium (94.2%), the urostyle (91.2%), and the tibio-fibula (90.1%) (Rey and Sanchiz, 2005) (Figure 3.8).

The literature on Iberian current populations document the predation of *Hyla* by the nocturnal owls *T. alba* and *Athene noctua*, and the diurnal kestrel *Falco tinnunculus* (Rey and Sanchiz, 2005; Diego-Rasilla and Ortiz-Santaliestra, 2009), but the digestion evidence and breakage in El Mirador accumulation and their percentages are not consistent with any of these species (Andrews, 1990; Pinto Llona and Andrews, 1999). If the criteria for amphibian taphonomy established by Pinto Llona and Andrews (1999) are used, the breakage category 2 documented in *H.* gr. *H. arborea* is coincident with the proposal for the tawny owl, *Strix aluco*, but this nocturnal raptor is ascribed to a higher digestion category (4). The available data for the digestion marks in anuran bones do not indicate any raptor with a digestion category 2, with category 1 being the closest value, which includes only the barn owl (*T. alba*), although its alterations to bones are practically null or very low (Pinto Llona and Andrews, 1999; Denys et al., 2018). On the other side, anuran remains associated with predation by carnivorous mammals show much higher degrees of digestion and breakage, categories 4-5 (e.g., Cobrante cave, Martín et al., 2009).

In analogous criteria established by Andrews (1990) for the digestion and breakage in the post-cranial skeleton of small mammals, breakage category 2 includes the spotted eagle-owl, *Bubo africanus*, and the eagle-owl, *Bubo bubo*, while digestion category 2 includes *S. aluco*, *B. africanus* and *B. bubo*. The possible assignment to *B. bubo* or *S. aluco*, based on the categorisations of Andrews (1990), would come into conflict with breakage category 3 and digestion category 5 proposed for *B. bubo* and breakage category 2 and digestion category 4 proposed for *S. aluco* in Pinto Llona and Andrews (1999). Though the rodent remains in the taphocenosis are very scarce for a better interpretation (25 MNE, 1.23%), in general, they show alterations compatible with a predator with a degree of light-intermediate modification, according to Andrews (1990), which is consistent with the anuran data. However, new data have shown the existence of seasonal variation between winter-summer in the degrees of digestion produced by *S. aluco*, specially in rodent molars and incisors (Andrews and Fernández-Jalvo, 2018).

Other factors could have influenced the taphonomy and generated differences between the comparison samples, such as the age of the predator, the time of digestion, the variations in tissues between amphibians and rodents, the number of preys in the intake or the consumed biomass. These variables demand greater caution in the identification of the predator. The same

applies to data on breakage, which should be considered with prudence, since they may be affected by post-depositional processes.

The eagle-owl is a generalist and opportunistic predator, which, on the Iberian Peninsula, hunts a wide range of herpetofauna species (*Bufo spinosus*, *Pelophylax perezi*, *Pelobates cultripes*, *Mauremys leprosa*, *Podarcis hispanica* sensu lato, *Psammodromus algirus*, *T. lepidus*, and Colubridae snakes) (Hiraldo et al., 1975; Pérez-Mellado, 1978; Vericad et al., 1976; Serrano, 1998; Penteriani and Delgado, 2016). Some individuals of *B. bubo* can specialise in certain prey groups, including anurans (Andrews, 1990). For example, in Hohe Tauern (Salzburg, Austria), frogs account for 48% of the MNI of the eagle-owl's diet while in Rogaland (Vestlandet, Norway) they represented 45.58% of the MNI. In both cases, they constitute the primary prey group (Hagen, 1950; Frey and Walter, 1986).

Although *S. aluco* is commonly considered a nocturnal species, much more than *B. bubo*, the record of lizards (*Lacerta schreiberi* and *Podarcis muralis*) in the diet of the tawny owl of León and Asturias indicates its predation on typically diurnal species (Nores, 1980; Alegre et al., 1989). Frogs represent 9.2% of the MNI in the diet of *S. aluco* of Scandinavia (Mikkola, 1995) and amphibians up to 10.40% in Poland (Romanowsky and Żmihorski, 2009). A similar percentage was obtained in a German macro-study of more than 72,000 preys of tawny owls, in which the anurans accounted for 10.2% of the MNI (Uttendörfer, 1952). Due to the large size of the accumulation (7.8x2.7x2.4 cm), it corresponds more accurately to a *B. bubo* pellet than to a *S. aluco* pellet (Mikkola, 1995), unless it was a very large tawny owl.

Regardless of the predator that generated the accumulation, the inclusion in the taphocenosis of at least 66 adult individuals of tree frogs suggests that it was formed during a period with an abundance of tree frogs in the environment. Currently, the Iberian Peninsula is inhabited by two species of tree frogs, the Mediterranean tree frog, *Hyla meridionalis*, which arrived recently from the Maghreb (Recuero et al., 2007), and the endemic Iberian tree frog, *H. molleri*, which belongs to the European *Hyla* gr. *H. arborea* taxon (Stöck et al., 2012). The most plausible option, for these biogeographical reasons, is that the tree frogs of El Mirador cave can be attributed to the native *H. molleri*.

In this species, the main concentrations of adults occur during the breeding season, when they gather in ponds with abundant vegetation between April and May (Lizana et al., 1989; Diego-Rasilla and Ortiz-Santaliestra, 2009). The reproduction begins with the arrival of males in groups of up to 20 per metre of shore. The males remain an average of 5.2 nights at the ponds, while 82% of females stay only one night (Márquez and Tejedo, 1990). The representation by sex in reproductive concentrations is skewed in favour of males, with biases ranging from 5.4:1 to 26.2:1 (García et al., 1987; Salvador and Carrascal, 1990).

The predation of an owl on *H. molleri* reproductive agglomerations could be the initial coprocenotic origin of El Mirador's taphocenosis. The avian raptor, which would use the cave as a nest or perch, opportunistically hunted

an abundant seasonal resource in the environment, linked to the wet weather of spring. The multiple choruses of the males, whose calls are audible more than a kilometre away (Stumpel, 1997), made them easy prey at night, particularly if the hunted individuals were united in mating axillary amplexus, in the which the male holds the female by the armpits for hours or days (García-París, 2004). This may explain the ratio of 1.36:1 in favour of the males identified in El Mirador, which is very low in comparison with the minimum ratio (5.4:1) documented currently (García et al., 1987). After digestion, the owl regurgitated the pellet inside El Mirador cave, at that time used as a burial site during the Chalcolithic (Vergès et al., 2016), which would have allowed it to be included within the sedimentary record without being destroyed or disintegrated by other human activities.

3.6. Conclusions

The almost monospecific accumulations of anurans, mainly frogs (*R. temporaria*), from European archaeological sites have often been cited as linked to human consumption (Bailon, 1997; Hüster, 2004; Chiquet, 2005; Kyselý, 2008). These are taphocenosis that appear in prehistoric settlements as a product of the exploitation of meat from *R. temporaria*, often with evidence of processing and cooking. The exception comes from the Late Pleistocene of Bois-Roche (France), where an accumulation of *P. punctatus* is associated with a natural catastrophic mortality (Cochard, 1998, 2004).

The case of the *Hyla* gr. *H. arborea* (*molleri*) taphocenosis MIR5-P21-n4 from El Mirador cave points to a different phenomenon. It was generated by the predation of a bird of prey (possibly a large tawny owl or eagle-owl) that opportunistically hunted an abundant seasonal resource. Both humans and avian raptors, despite the differences, hunt anurans during the breeding period, in which they are massively concentrated in bodies of water. These findings indicate the great importance that such small prey had in the subsistence diets in the past, and how the life cycles of small animals were exploited. The exceptional stratigraphy of El Mirador cave, which has provided more coprocenotic taphocenosis of microfauna with the abundant presence of herpetofauna, will serve to determine the importance of amphibians and reptiles in the animal trophic chains of the Holocene. Finally, it is necessary to highlight the importance and the need to study amphibian taphonomy in greater depth, including modern samples. Amphibian evidence is scarce and largely overlooked despite being, as this paper proves, essential in understanding the origin of the accumulations and their role in humans and non-human predators' diets in the past.

Supplementary data

Appendix 4.- Systematic description of the herpetofaunal remains from El Mirador pellets (MIR4 and MIR5) (pages 215-231).

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BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Chapter 4

Seasonality, predation and landscape anthropisation in small vertebrate accumulations from the mid-late Holocene transition of El Mirador cave (Atapuerca, Spain)

Abstract

Birds of prey and carnivorous mammals are among the primary accumulating agents of faunal remains in karst sites. The remains of microvertebrates contributed by these predators tend to be dispersed in the sediment by means of disintegration processes. At El Mirador cave (Atapuerca, Spain), twenty small accumulations have been recovered in the Chalcolithic (MIR5) and Bronze Age (MIR4) levels, which contain abundant remains of small vertebrates: birds, rodents, and especially, herpetofauna. The previous taphonomic study of the most significant accumulation identified it as a pellet produced by a medium-large owl. Contemporary literature on the diet of birds of prey suggests seasonal variations in the faunal composition of their diets, the presence of which is diminished in the archaeo-paleontological record due to processes of disintegration and dispersion. In this chapter, we analyse the accumulations of El Mirador by means of statistical analyses, examining qualitative and quantitative changes in their composition to infer possible seasonal differences. These analyses allow us to study the impact that the biases caused by seasonality, predation, ethology, phenology and the annual activity of preys can have on palaeoenvironmental and palaeoclimatic reconstructions undertaken by means of herpetofauna and small-mammal associations in contexts in which they have not undergone intermixing processes. The results show variations in the taxonomic composition and the number of preys, which are linked to the seasonal period between the end of winter and summer marking the end of hibernation and the reproductive cycles of amphibians and reptiles. The palaeoenvironmental reconstruction using the different seasonal associations indicates changes in the distribution of primary habitats, with increased wet areas between late winter and mid-spring and increased aridity between mid-spring and summer. In contrast, the palaeoclimatic reconstruction did not reveal significant differences in annual or monthly temperatures, although higher precipitation was documented in the associations assigned to winter–mid-spring. The unique faunistic composition of the accumulations, primarily made up of reptiles and amphibians, is interpreted as a collateral effect of the human impact during the Chalcolithic-Bronze Age transition in the Atapuerca area, which forced the owl to prey on less optimal but more seasonally abundant prey.

4.1. Introduction

Caves and other karst spaces such as rock shelters or shaft caves were among the most widely used habitat, burial and worship-ritual spaces for human communities throughout prehistory (Bonsall and Tolan-Smith, 1997). Other vertebrate animals have also used karstic sites, either in alternation

with humans or sometimes cohabiting in the same spaces, and have added their remains to the stratigraphic sequence. Small to medium-sized carnivorous mammals and birds of prey stand out among the contributors of microvertebrate remains at archaeo-paleontological cave sites (Andrews, 1990; Pinto Llona and Andrews, 1999; Stoetzel et al., 2012; Fernández-Jalvo and Andrews, 2016; Denys et al., 2018) through the phenomenon known as *coprocoenosis*, in which they leave faunal remains at these sites after predation and digestion (Mellet, 1974).

Birds of prey (Falconiformes, Accipitriformes, and Strigiformes) expel bone remains and other undigested organic materials after initial digestion in a tightly-packed mass called a *pellet* (Mikkola, 1995). The first paravian pellets documented in the fossil record come from the Jurassic and Cretaceous periods, contemporaneous with the great diversification of the theropod dinosaur clade Paraves and the emergence of the first true birds (Sanz et al., 2001; Zheng et al., 2018). Their complete conservation is very rare in the paleontological and archaeological record, although pellets are occasionally accumulated in large taphocenoses of small bones (De Cupere et al., 2009). In most cases, the faunal remains from pellets appear dispersed inside the sediment, affected by pre-depositional and post-depositional taphonomic processes that promote disintegration, such as weathering, trampling and water streams (Andrews, 1990; Fernández-Jalvo and Andrews, 2003; García-Morato et al., 2019). This disaggregation effect can be seen in the majority of Quaternary sites, such as Sima del Elefante (Blain et al., 2010), Valdavara-1 (López-García et al., 2011a), Cova del Gegant (López-García et al., 2012a), Mollet Cave (Maroto et al., 2012), and El Harhoura 2 (Stoetzel et al., 2012), where the microvertebrate remains (or some of them) were contributed by birds of prey. Moreover, coprocoenotic remains are mostly dispersed in the sediment together with remains from other sources, which minimises the biases that predator contributions can sometimes give rise to in the interpretations of the past.

In El Mirador cave (Burgos, Spain), twenty concentrated accumulations containing microfaunal remains with a significant abundance of herpetofauna were recovered from levels MIR4 and MIR5 (Figure 4.1), dated to the Chalcolithic to the Bronze Ages (Vergès et al., 2016). To determine their origin, a taphonomic analysis was performed on the largest accumulation (MIR5-P21-n4). The results identified the accumulation as a bird pellet produced by a category 2 predator, possibly the owls *Bubo bubo* or *Strix aluco*, which was preserved intact due to the special conditions of the cave during the Chalcolithic period, when it was used as a burial space (Chapter 3). Additionally, the quantitative taxonomic composition of this pellet points to the seasonal predation of *Hyla* gr. *Hyla arborea* (*Hyla molleri*) during a period in which this tree frog would have been abundant in the wet and temperate landscape around the cave (Chapter 3).

In recent years, the use of Quaternary microvertebrate assemblages

Figure 4.1.- Pellets from El Mirador cave, *in situ*. **A:** accumulation MIR5-P21-n7, from the central test pit. **B**: accumulation MIR204-S34-n5, from the northern section.

for palaeoenvironmental and palaeoclimatic reconstructions has received considerable attention in the literature with the introduction of the mutual ecogeographic range and habitat weighting methods (Blain, 2009; Blain et al., 2008, 2009a, 2016, 2018; Agustí et al., 2009; López-García et al., 2011a). These methods use microfaunal concurrences to calculate temperature and rainfall data and to determine the primary landscape environments surrounding the studied sites using actualistic data on the species that are present in the fossil assemblages. However, current data about the diets of birds of prey indicate that their composition varies with the seasons and over the years, according to seasonal-annual cycles and/or due to environmental changes (Pérez-Mellado, 1978; Zerunian et al., 1982; Donázar, 1989; Lara, 1995; García and Cervera, 2001; Andrews and Fernández-Jalvo, 2018). These data suggest the existence of possible representation biases in the archaeological and paleontological record from disaggregated bird pellets, such as the under-representation or absence of some taxa and the over-representation of others. These biases could lead to alterations in reconstructions of the past and the degrees of confidence and accuracy that can be ascribed to them, especially in assemblages made up of few specimens. They can also particularly affect Holocene archaeological sites with very marked stratigraphy containing successive chronocultural periods in defined levels representing chronologically short phases compared to the Pleistocene and earlier records. These short-time levels are therefore more likely to be biased since the contributions are attributed to a shorter period of time.

The individualised preservation of multiple accumulations from El Mirador cave interpreted as owl pellets containing great taxonomic variety (at least 20 different taxa of amphibians, squamate reptiles, birds and mammals) and a high number of individuals (350 MNI) has allowed us to approach the problem of representation bias in a coprocoenotic record and explore its effects on palaeoenvironmental and palaeoclimatic reconstructions. The data derived from the study of these pellets were compared with those yielded by the associations of small mammals from El Mirador, and have allowed us to examine the implications about the evolution of the landscape in relation to the environmental and climatic changes of the Holocene and the influence of human impact (López-García, 2008; Bañuls-Cardona et al., 2013, 2017a, 2017b).

4.2. El Mirador cave and the 4.2 ka event

El Mirador cave (*Cueva de El Mirador*) is located on the slopes of the southern tip of the Sierra de Atapuerca, within the municipality of Ibeas de Juarros, and is part of the Atapuerca karst system. It is located at 42º 20' 58" N and 03º 30' 33" W and it rises to 1,033 m.a.s.l. (Figure 3.1) over the middle basin of the Arlanzón River. The cave is currently 23 metres wide by 4 metres high and 15 metres deep, and is configured as an open shelter due to the collapse of the vault (Vergès et al., 2002). The vegetation

of the surrounding areas is characterised by cereal croplands of mixed open Mediterranean continental forests of *Quercus ilex* subsps. *rotundifolia* and *ballota* (evergreen oak) and *Quercus faginea* (deciduous Portuguese oak), together with communities of *Quercus pyrenaica* (marcescent oak) on the fluvial terraces and siliceous soils, as well as signs of Atlantic-Eurosiberian influences in the presence of *Erica vagans* (wandering heath) and *Calluna vulgaris* (common heather) (Rodríguez et al., 2016).

Between 1999 and 2008, the archaeological work focused on a 6 m² test pit located in the central area of the western half of the cave, where a large Holocene succession was found, consisting of 24 differentiated archaeological levels (Figure 3.1): Levels MIR1 and MIR2 are mixed layers formed by animal burrows and modern anthropogenic actions; MIR3 is partially disturbed, with mixed remains from the Middle to Late Bronze Age; MIR4 is a substantial level from the Middle Bronze Age, which includes at its base a secondary burial of cannibalised human bones from the Early Bronze Age that were buried during the Middle Bronze Age (Cáceres et al., 2007; Vergès et al., 2016); MIR5 is a thin level with scarce anthropogenic contributions, but it is rich in small vertebrate remains (Vergès et al., 2002). The remaining Holocene levels (MIR6–MIR24) are assigned to the Neolithic and are mostly made up of livestock pen waste, mainly *fumiers*, with the Late Neolithic represented at the top of the sequence (including MIR6) (Angelucci et al., 2009; Vergès et al., 2016).

New dating obtained from the rodent bones contained in pellet MIR5-P21-n4 (Beta-521985: 4,530–4,417 cal BP; Table 4.1) indicates that it is contemporaneous with the Chalcolithic collective burial in MIR203 (4,880–4,480 cal BP and 4,550–4,390 cal BP) in the northern section of the cave (sector 200) (Ceperuelo et al., 2014, 2015; Lozano et al., 2015; Vergès et al., 2016). The sedimentation in MIR5 is attributed to exclusively natural processes and occurred very slowly, around 0.1 mm/year, in contrast to the 4-5 mm/year of the levels MIR11–16, caused by the anthropic activity of the *fumiers* (Vergès et al., 2008). This low sedimentation rate has been associated with the interruption of anthropogenic contributions during MIR5 (Vergès et al., 2002), proof of little to no human activity in the cave during the deposition of the sediments, as the pellets would have been rapidly disintegrated by trampling or other actions associated with human occupation. In western sector 100, another individual burial of a young man from the Middle Bronze Age (MIR106) was found on a ledge of the karst wall, dated 3,670–3,470 cal BP (Vergès et al., 2016). This burial is contemporaneous with the base of MIR4 (3,730–3,530 cal BP) (Vergès et al., 2002, 2016).

The regional climatic context in which both MIR4 and MIR5 are framed was affected by the 4.2 ka BP event, which although it occurred on a global scale, varied greatly in its climatic expression at the local and regional level (Magny et al., 2009, 2013; Bini et al., 2019). Different palaeohydrological and

Level	Material	Identification	Laboratory number	Conventional radiocarbon age BP	2σ calibrated BC	2σ calibrated BP	$^{13}C/^{12}C$ ratio
MIR4 (roof)	Charcoal	*Quercus* sp. evergreen	Beta-154894	3040 ± 40	1440 - 1120	3390 - 3070	-23.9‰
MIR4 (base)	Charcoal	*Quercus* sp. deciduous	Beta-153366	3400 ± 40	1780 - 1580	3730 - 3530	-23.8‰
MIR106	Human bone	*Homo sapiens*	Beta-296226	3340 ± 30	1720 - 1520	3670 - 3470	-19.4‰
MIR4 (pit)	Human bone	*Homo sapiens*	Beta-153366	3670 ± 40	2060 - 1820	4010 - 3770	-19.3‰
MIR4 (pit)	Human bone	*Homo sapiens*	Beta-182042	3830 ± 40	2270 - 1990	4220 - 3940	-18.8‰
MIR4 (pit)	Human bone	*Homo sapiens*	Beta-182041	3900 ± 40	2380 - 2100	4330 - 4050	-19.2‰
MIR5 (pellet)	**Rodent bone**	**Rodentia indet.**	**Beta-521985**	**4010 ± 30**	**2581 - 2468**	**4530 - 4417**	**-22.4‰**
MIR203	Human bone	*Homo sapiens*	Beta-296225	4000 ± 30	2600 - 2440	4550 - 4390	-18.9‰
MIR203	Human bone	*Homo sapiens*	Beta-296227	4220 ± 30	2930 - 2530	4880 - 4480	-18.7‰
MIR6	Charcoal	*Quercus* sp. evergreen	Beta-153367	4780 ± 40	3680 - 3400	5630 - 5350	-23.5‰

Table 4.1.- Datings from the upper levels of the central test pit sequence, El Mirador cave. The calibration of radiocarbon age to calendar years is based on the High Probability Density Range Method (HPD): Intcal'13 curve (Ramsey, 2009; Reimer et al, 2013).

palaeomarine proxies suggest an arid phase in the southern central Mediterranean between 4,500 to 4,000 BP, while the northern regions experienced increased humidity north of 40º latitude (Magny et al., 2013). An isotopic study of speleothems from central Italy and their comparison with central Mediterranean records of between 4,300 to 3,800 BP again points to regional differences, with drier conditions in the central and southern areas of the Italian Peninsula but no significant changes in temperatures, while the northern zones and the Alps tended towards a colder and wetter climate. In this same study, an increase in aridity was associated with a decrease in precipitation during the summer, which would have led to summer drought (Zanchetta et al., 2016).

The results of another multiproxy study in the Mediterranean Basin suggest a drier seasonality at the regional level for the same period, both in winter and summer, although in some areas the conditions remained as or even more humid (Bini et al., 2019). At a local level, these increments in aridity may have been related to torrential rain events, which would have increased erosion (Cartier et al., 2019; Bini et al., 2019). Regional pollen research in the central Mediterranean zone depicts the regionalisation of climate and vegetation cover changes as of the 4.2 ka BP event according to latitude: the northern regions (43º–45º) underwent a very slight decrease in precipitation, though the plant composition remained unchanged; in the central area (39º–43º), there was both a decrease in precipitation and a decrease in tree pollen, though this pattern is imprecise in some sequences; while in the southern regions (36º–39º), there was a very marked decrease in tree pollen as well as marked human impact. The increase in aridity in the southern regions is due to the influence of the north African climate, which is characterised by high pressure resulting in limited rainfall (Di Rita and Magri, 2019).

The data available for the Iberian Peninsula also point to great variation at the regional level. A macro study of the peninsula showed an increasing trend towards aridity due to a decrease in winter rainfall from 6,000 to 3,000 cal BP, which was aggravated during the 4.2 ka BP event by the severe decline in summer rainfall and/or increase in summer drought. At the same time, the area experienced a drop in winter temperatures between 4,400 and 4,000 cal BP (Schirrmacher et al., 2020). Other evidence for the western Mediterranean suggest a cooling phase between 4,300 and 3,800 cal BP, with a double cooling peak during the 4.2 ka BP event (Català et al., 2019). Regional variability, therefore, is repeated on the Iberian Peninsula, with the southern and eastern Mediterranean regions undergoing more abrupt changes during this climate event, and the northern areas of Eurosiberian and Atlantic influence remaining more stable (Lillios et al., 2016).

4.3. Material and methods

4.3.1. *Sampling*

During the 2000 excavation campaign in El Mirador cave, twenty accumulations were identified containing sub-fossil microvertebrate remains from the base of level MIR4 and from level MIR5 in grids P21, P22, Q20, and Q21 of the central test pit (Figure 4.2). The depth range (Z) is from 1267 to 1287 (Table 4.2). These taphocenoses were isolated, their locations were recorded, and they were then removed from the excavation surface. The bone remains were subsequently isolated in the micropaleontology laboratory of the Catalan Institute of Human Paleoecology and Social Evolution (IPHES) through screening with a running-water washing system and decreasing mesh sizes (5 mm, 2 mm and 0.5 mm). They were identified taxonomically using a binocular magnifier. A total of 6,579 bone elements

Pellet	Level	Square	Number	Location		
				X	Y	Z
MIR4-Q21-n227	MIR4	Q21	227	63	19	1275
MIR4-Q21-n228	MIR4	Q21	228	63	23	1274
MIR4-Q21-n231	MIR4	Q21	231	58	29	1282
MIR4-Q21-n233	MIR4	Q21	233	58	5	1283
MIR4-Q21-n234	MIR4	Q21	234	60	30	1282
MIR4-Q21-n235	MIR4	Q21	235	47	30	1281
MIR4-P21-n243	MIR4	P21	243	87	25	1267
MIR4-Q21-n245	MIR4	Q21	245	29	32	1286
MIR4-P21-n246	MIR4	P21	246	38	25	1269
MIR4-P21-n252	MIR4	P21	252	81	69	1274
MIR4-Q20-n261	MIR4	Q20	261	24	90	1285
MIR4-Q20-n262	MIR4	Q20	262	28	93	1287
MIR4-P21-n264*	MIR4	P21	264	30	15	1275
MIR4-P21-n267	MIR4	P21	267	59	10	1272
MIR4-P22-n380	MIR4	P22	380	51	76	1278
MIR5-P22-n1	MIR5	P22	1	29	10	1273
MIR5-P22-n2	MIR5	P22	2	50	41	1278
MIR5-P21-n4	MIR5	P21	4	25	38	1284
MIR5-P21-n7	MIR5	P21	7	94	48	1285
MIR5-P22-n13	MIR5	P22	13	38	5	1287

Table 4.2.- Accumulations of small vertebrates from MIR4 and MIR5 levels and their stratigraphic positions.

were counted. Accumulation MIR4-P21-n264 has been partially preserved in its entirety for future taphonomic studies, and is not included in this paper

4.3.2. *Taxonomic identification*

The following elements were used to identify the herpetofauna: the parasphenoids, frontals, humeri and the vertebrae for caudates (Buckley and Sanchiz, 2012; Gleed-Owen, 1998; Ratnikov, 2015); frontoparietals, squamosals, scapulae, humeri, vertebrae and ilia for anurans (Bailon, 1999; Blain and Arribas, 2017); the maxillae, pterygoids, frontals, parietals, quadrates, coronoids, dentaries and vertebrae for non-ophidian squamates (Anguidae, Scincidae, Lacertidae) (Barahona, 1996; Barahona and Barbadillo, 1997; Gleed-Owen, 1998; Blain, 2009; Caputo, 2004); and the vertebrae for snakes (Szyndlar, 1984). For small mammals, the first lower molar was used for the Arvicolinae, and isolated teeth for *Apodemus sylvaticus* (Chaline, 1972; Cuenca-Bescós et al., 1997,

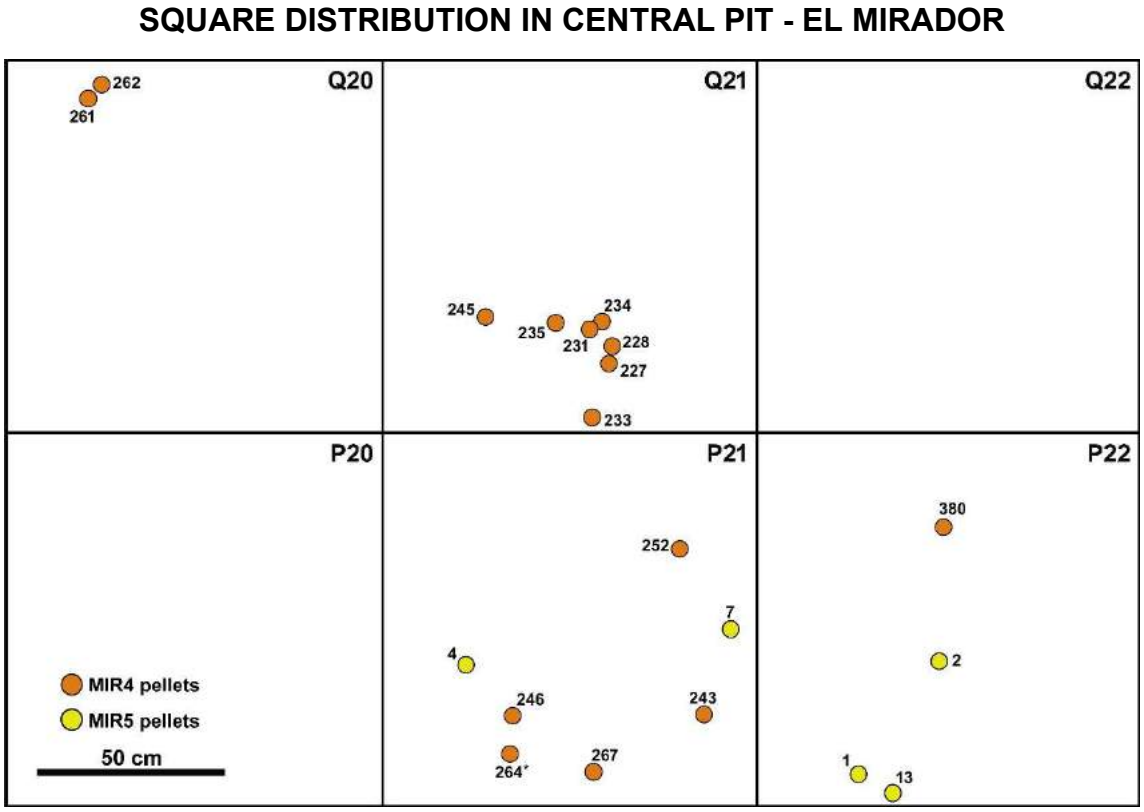

Figure 4.2.- Position of the accumulations of small vertebrates from MIR4 and MIR5 levels in the grids of the central test pit sequence, El Mirador cave.

2008) and for *Sorex araneus* (Reumer, 1984; Cuenca-Bescós et al., 2008). Modern specimens from the reference collections of the Museo Nacional de Ciencias Natural of Madrid (MNCN-CSIC) and the IPHES were used as comparison material.

4.3.3. *Statistical analysis*

Two data matrices were created to study the differences in the faunistic composition of the pellets and to infer possible trends in predation for each level (MIR4 and MIR5). The different pellets are shown in the columns, and the taxa are shown in the rows along with their minimum number of individuals (MNI). Unlike other analyses based on presence/absence, in this case, the quantitative values of individuals by species in the data matrices are maintained. The aim is to infer percentage variations in representativeness and not only proximity relationships by taxonomic composition.

In addition, some corrections have been applied in order to reduce dispersion and facilitate interpretation. Lacertidae indet. (small), Lacertidae indet. (medium-sized) and *Vipera* sp.

(*Vipera aspis/seoanei*) are included because they respond to different habitat contexts and have environmental significance despite the lack of their taxonomic definition.

Due to the impossibility of determining most of the micromammals in the sample to the species level, all the identified arvicoline voles (Arvicolinae indet., *Microtus* sp., *Microtus agrestis*, *Microtus arvalis* and *Terricola duodecimcostatus*) were grouped in the clade Arvicolinae (subfamily). However, Bufonidae indet. was not added because it can correspond to two species with very different requirements (*Bufo spinosus* and *Epidalea calamita*).

A correspondence analysis (CA) was used on the data matrices (Greenacre, 2010). CA is the recommended method for comparing assemblages (assigned to column) and the taxa they include (assigned to rows) in an equivalent way. In this paper, the objective is to identify the relationships of proximity between the different taxa documented in the owl pellets, grouping them more closely the higher the degree of concurrence against the comparatively more atypical taxa, which will appear in an eccentric position in relation to the rest of the sample. The associations of the pellets are also organised following the same pattern, according to the greater number of concurrences in their compositions. The Paleontological Statistics program (PAST3) was used for all statistical analyses (Hammer et al., 2001).

4.3.4. *Palaeoenvironmental reconstruction*

We used the habitat weighting method (Evans et al., 1991; Andrews, 2006; adapted by Blain et al., 2008 for amphibians and squamate reptiles) for the palaeoenvironmental reconstruction. This method employs a percentage distribution in five different habitats preferentially occupied by each identified species, calculated based on the MNI per taxon (Table 4.3).

The five habitats included are: *Open Dry*: open dry environments, spaces with little vegetation or vegetation of low height and subject to seasonal changes in humidity, especially during the summer drought; *Open Humid*: open wet environments, which include open areas with low perennial and dense vegetation that remains wet throughout the year; *Woodland*: shrublands and forests, environments with greater plant cover reaching comparatively greater heights, from medium shrublands to closed forests, including the margins of these areas; *Rocky*: open environments with low or scarce vegetation, poor substrate and an abundance of emerged rock and stones; *Water Edge*: aquatic and periaquatic environments, permanent or temporary bodies of water (rivers, lakes, streams, ponds, etc.) and their immediate surrounding areas, with hydrophilic and hygrophilous vegetation.

The percentage data for each species are provided in Blain et al. (2008, 2010, 2010b, 2011a, 2011b, 2011c, 2013) and López-García et al., (2011a) for herpetofauna, and López-García et al.

Species	Common name	Open Dry	Open Humid	Woodland	Rocky	Water Edge
Lissotriton helveticus	Palmate newt		0.2			0.8
Triturus marmoratus	Marbled newt		0.4	0.2		0.4
Alytes obstetricans	Common midwife toad		0.6	0.2		0.2
Pelobates cultripes	European spadefoot toad	0.8				0.2
Hyla molleri (*Hyla* gr. *H. arborea*)	Iberian tree frog		0.5	0.2		0.3
Bufo spinosus (*Bufo* gr. *B. bufo*)	Spiny common toad	0.1	0.3	0.4		0.2
Epidalea calamita	Natterjack toad	0.65			0.25	0.1
Rana temporaria	Common brown frog		0.4	0.4		0.2
Anguis fragilis	Slowworm		0.25	0.75		
Chalcides striatus	Western three-toed skink		0.4	0.3	0.3	
Lacerta bilineata	Western green lizard		0.5	0.4	0.1	
Timon lepidus	Ocellated lizard	0.5			0.5	
Coronella austriaca	Smooth snake		0.5	0.25	0.25	
Vipera aspis/seoanei	Viper		0.25	0.5	0.25	
Microtus agrestis	Field vole		0.5	0.5		
Microtus arvalis	Common vole	0.5		0.5		
Terricola duodecimcostatus	Mediterranean pine vole		0.25	0.5	0.25	
Apodemus sylvaticus	Wood mouse			1		
Sorex araneus	Common Eurasian shrew		0.5	0.5		

Table 4.3.- Habitat weighting values for the herpetofauna and small-mammal species from the pellets of MIR4 and MIR5, El Mirador cave.

(2011a) and Bañuls-Cardona et al. (2011) for mammals. For *Lacerta* (cf.) *bilineata*, without a previous record, new parameters were created based on Ortiz-Santaliestra et al. (2011), Masó and Pijoan (2011) and Gosá and Rubio (2015).

4.3.5. *Palaeoclimatic reconstruction*

The palaeoclimatic reconstruction is based on the mutual ecogeographic range method (MER), which quantifies rainfall and temperatures and, from these, the different bioclimatic indices using the concurrence of microvertebrate species from the same level (Blain, 2009; Blain et al., 2009a, 2016). For this purpose, the locations on the Iberian Peninsula where the same species currently live are identified as appearing in concurrence at the same level of the archaeological record, using the geographical division into 10 x 10 km UTM squares. In order to avoid distortions in the results, the grids affected by disturbing factors, such as the industrial anthropisation of the landscape or an extreme difference in elevation from that of the El Mirador site, were excluded.

The main distribution atlases of amphibians, reptiles and mammals in the Iberian Peninsula were used for the MER (Palomo et al., 2007; AHE, 2020) in conjunction with the climatic parameters of the weather stations located in the grids where the current concurrences are located (Climatic-Data.org). As an current reference sample, we used the climate data obtained between 1982 and 2012 in Ibeas de Juarros, the closest town to El Mirador cave (2.2 km, west). The data obtained were the mean annual temperature (MAT), mean monthly temperature for each month of the year, and the mean annual precipitation (MAP), thus representing a total of 26 parameters.

4.4. Results

4.4.1. *Small vertebrates' content from the MIR4 and MIR5 pellets*

A total of 14 pellets from MIR4 and five from MIR5 have been documented, for a minimum number of individuals (MNI) of 350 (Figure 4.3, Tables 4.5 and 4.6; Appendix 4). The faunal remains are distributed in at least 20 different taxa with generic or specific level adscription. These are the caudates *Lissotriton helveticus* (34 MNI) and *Triturus marmoratus* (15 MNI); and the anurans *Alytes obstetricans* (2 MNI), *Pelobates cultripes* (6 MNI), *Hyla* gr. *Hyla arborea* (136 MNI), *Epidalea calamita* (6 MNI), *Bufo* gr. *B. bufo* (5 MNI), and *Rana temporaria* (15 MNI). The reptiles include the squamates *Anguis fragilis* (12 MNI), *Chalcides striatus* (42 MNI), *Lacerta* cf. *bilineata* (7 MNI), *Timon lepidus* (4 MNI), *Coronella austriaca* (6 MNI), and *Vipera* sp. (*Vipera aspis*/*seoanei*) (1 MNI) (Appendix 4). In addition, at least nine Lacertidae individuals could not be identified more precisely due to a lack of diagnostic criteria. These are small (3 MNI) and medium-sized (6 MNI) lacertids, which may correspond to both adult and juvenile individuals of one or more species.

The mammals are represented by rodents and insectivores. The most prevalent clade is Rodentia, especially the arvicoline voles, *Microtus agrestis* (4 MNI), *Microtus arvalis* (4 MNI), and *Terricola duodecimcostatus* (3 MNI), but also the murid *Apodemus sylvaticus* (6 MNI). However, a high number of individuals could not be determined beyond the subfamily level (Arvicolinae indet., 24 MNI) or order level (Rodentia indet., 3 MNI) owing to the lack of preserved diagnostic molars. The only insectivore identified is the shrew *Sorex araneus* (1 MNI), determined by means of a single first left upper molar from MIR4-P21-n252 (Figure 4.3.AI). Likewise, the presence of birds (2 MNI) has been documented in the pellets through a right tarsometatarsus from MIR4-Q21-n245 (Figure 4.3.AC.1-2) and a right carpometacarpus from MIR4-P22-n380 (Figure 4.3.AD 1-2).

There are differences in the species number and the representation percentages of each taxon between the pellet assemblages of MIR4 and MIR5. One of the most notable of these differences is the higher percentage of *Hyla* gr. *H. arborea* in MIR5, where this tree frog represents 66.33% of the association, when compared to MIR4 (7.65%). In contrast, other taxa are more

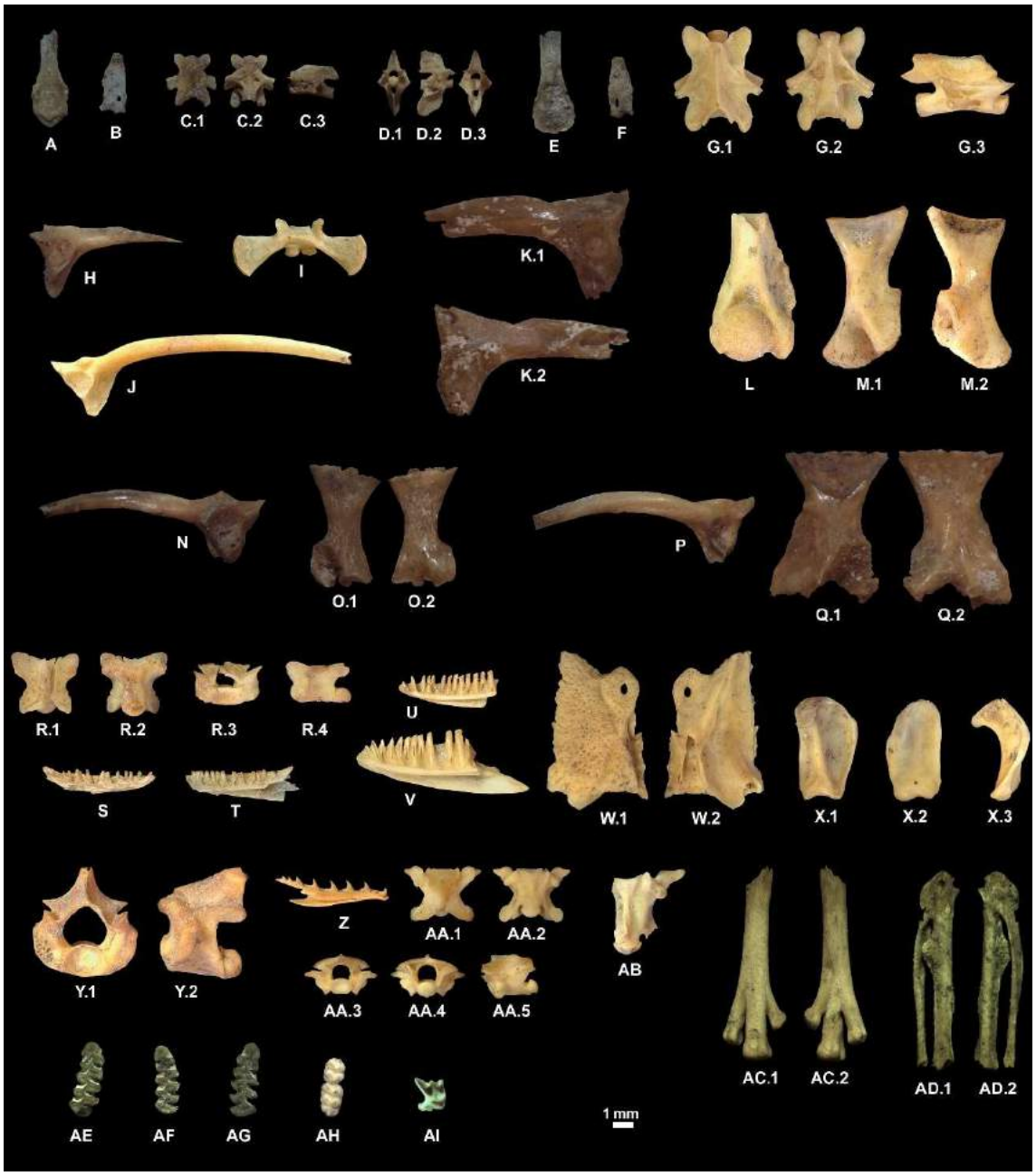

Figure 4.3.- Small vertebrates from the accumulations of MIR4 and MIR5 levels, El Mirador cave. **A-D:** *Lissotriton helveticus*, **A:** parasphenoid, dorsal view, **B:** right orbitosphenoid, medial view, **C:** trunk vertebra, dorsal (C.1), ventral (C.2) and lateral (C.3) views, **D:** caudal vertebra, anterior (D.1), lateral (D.2) and posterior (D.3) views (MIR4-Q20-n262); **E-G:** *Triturus marmoratus*, **E:** parasphenoid, dorsal view, **F:** left orbitosphenoid, medial view (MIR4-Q20-n262), **G:** trunk vertebra, dorsal (G.1), ventral (G.2) and right lateral (G.3) views (MIR5-P21-n4); **H:** *Alytes obstetricans*, right ilium, lateral view (MIR5-P21-n7); **I-J:** *Hyla* gr. *H. arborea*, **I:** sacral vertebra, dorsal view, **J:** right ilium, lateral view (MIR5-P21-n4); **K:** *Pelobates cultripes*, left ilium, lateral (K.1) and medial (K.2) views (MIR5-P21-n7); **L-M:** *Rana temporaria*, **L:** right humerus, ventral view, **M:** right scapula, ventral (M.1) and dorsal (M.2) views (MIR5-P21-n4); **N-O:** *Epidalea calamita*, **N:** left ilium, lateral view, **O:** right scapula, dorsal (O.1) and ventral (O.2) views (MIR4-Q21-n233), **(cont.)**

(cont.) P-Q: *Bufo* gr. *B. bufo*, **P:** left ilium, lateral view, **Q:** left scapula, dorsal (Q.1) and ventral (Q.2) views (MIR5-P21-n7); **R:** *Anguis fragilis*, trunk vertebra, dorsal (R.1), ventral (R.2), lateral (R.3) and anterior (R.4) views (MIR5-P21-n4); **S-T:** *Chalcides striatus*, **S:** left dentary, medial view; **T:** right dentary, medial view (MIR5-P21-n4); **U:** Lacertidae indet. (small size), right dentary, medial view (MIR5-P21-n4); **V-X:** *Lacerta* cf. *bilineata*, **V:** right dentary, medial view; **W:** parietal, dorsal (W.1) and ventral (W.2) views; **X:** quadrate, anterodorsal (X.1), posterodorsal (X.2) and lateral (X.3) views (MIR5-P21-n4); **Y:** *Timon* cf. *lepidus*, cervical vertebra, anterior (Y.1) and left lateral (Y.2) views (MIR5-P21-n4); **Z-AA:** *Coronella austriaca*, **Z:** left dentary, medial view (MIR5-P21-n4); **AA:** trunk vertebra, dorsal (AA.1), ventral (AA.2), anterior (AA.3), posterior (AA.4) and left lateral (AA.5) views (MIR5-P21-n4); **AB:** *Vipera* sp., trunk vertebra, ventral view (MIR5-P21-n4); **AC-AD:** Aves indet., **AC:** right tarsometatarsus, dorsal (AC.1) and ventral (AC.2) views (MIR4-Q21-n245), **AD:** right carpometacarpus, dorsal (AD.1) and ventral (AD.2) views (MIR4-P22-n380); **AE:** *Microtus agrestis*, first left lower molar, occlusal view (MIR4-P21-n246); **AF:** *Microtus arvalis*, first left lower molar, occlusal view (MIR4-P21-n246); **AG:** *Terricola duodecimcostatus*, first right lower molar, occlusal view (MIR5-P22-n1); **AH:** *Apodemus sylvaticus*, first and second right lower molars, occlusal view (MIR4-P21-n246); **AI:** *Sorex araneus*, first left upper molar, occlusal view (MIR4-P21-n252).

abundant in MIR4, such as newts, skinks and voles. The number of species remains stable at both levels with a total of 17–18 different identified taxa, of which 15 concur in both MIR4 and MIR5. MIR5 presents a greater number of herpetofauna species, with the midwife toad *A. obstetricans* and the snake *Vipera* sp. (V. *aspis*/*seoanei*), while the field vole *M. agrestis* and common shrew *S. araneus* appear in the MIR4 pellets. However, the apparent absence of *M. agrestis* in MIR5 may be linked to the problematic identification of the Arvicolinae remains due to the absence of diagnostic elements.

4.4.2. *Taxonomic comparison between pellets and species*

4.4.2.1. *MIR4*

In the correspondence analysis of species from MIR4, the horizontal axis is interpreted in a left-right direction from higher to lower moisture, while the horizontal axis shows differences in a top-bottom direction from open to forested areas (Figure 4.4.A). This results in a graphic representation of the species with the formation of three large groups: one located in the upper left quadrant, made up of the aquatic or highly hygrophilous species *L. helveticus*, *T. marmoratus, Bufo* gr. *B. bufo* (*B. spinosus*), *R. temporaria* and *S. araneus*; another one in the upper right quadrant made up of species with preferences for sunny and open habitats, *A. fragilis*, *C. striatus*, *T. lepidus*, *E. calamita* and *P. cultripes*, with an internal organisation that follows the criterion of the horizontal axis (wet-dry); and a third group located in the bottom half comprised of species with preferences for environments with a greater plant cover than those of the second group: *Hyla* gr. *H. arborea*, *Lacerta* cf. *bilineata*, *C. austriaca*, the arvicoline voles and *A. sylvaticus* (Figure 4.4.A).

Level	MIR4														
Square	P21				P22	Q20		Q21							Total
Pellet	243	246	252	267	380	261	262	227	228	231	233	234	235	245	All
Lissotriton helveticus		1	8	1		5	12	1	2				1		31
Triturus marmoratus			2	2		3	3								10
Pelobates cultripes											1		1		2
Hyla gr. *H. arborea*		1	1	1	1	3	2	2				1		1	13
Bufo gr. *B. bufo*						1									1
Epidalea calamita	1								1	1	2				5
Bufonidae indet.				1					1						2
Rana temporaria						5	6						1		12
Anguis fragilis	2		1		1				1	1		1			7
Chalcides striatus			1	1	1		1	5	6	12	1	2	7	2	39
Lacerta cf. *bilineata*	1		1												2
Timon lepidus												1	1		2
Lacertidae indet. (small size)														1	1
Lacertidae indet. (middle size)					1	1	1	1	2						6
Coronella austriaca		1		1					1						3
Ophidia indet.			1												1
Aves indet.					1									1	2
Rodentia indet.	2												1		3
Arvicolinae indet.		8		1			2	1	1	1				1	15
Microtus agrestis		3	1												4
Microtus arvalis		2				1									3
Terricola duodecimcostatus														1	1
Apodemus sylvaticus		3												1	4
Sorex araneus			1												1
TOTAL (NMI)	6	19	17	8	5	19	27	10	15	15	4	5	12	8	170

Table 4.5.- Distribution of small vertebrates according to the minimum number of individuals (MNI) by pellets from MIR4, El Mirador cave.

The graphic representation of the correspondence analysis for the MIR4 pellets is organised differently, but retains the same dynamics in which the taxa with higher representation values determine the position and the groups are formed by habitat preferences (Figure 4.4.B). The first group is made up of the pellets in which hygrophilous taxa predominate and, more specifically, have a marked presence of *T. marmoratus* and *L. helveticus* (MIR4-P21-n246, MIR4-P21-n252, MIR4-Q20-n261, MIR4-Q20-n262 and MIR4-P21-n267). The second group includes pellets primarily made up of species with preferences for open lands

Level	**MIR5**					
Square	**P21**		**P22**			**Total**
Pellet	**4**	**7**	**1**	**2**	**13**	**All**
Lissotriton helveticus		**1**	**1**	**1**		**3**
Triturus marmoratus	**3**		**1**	**1**		**5**
Alytes obstetricans		**1**		**1**		**2**
Pelobates cultripes		**3**		**1**		**4**
Hyla* gr. *H. arborea	**66**	**1**	**2**	**33**	**21**	**123**
Bufo* gr. *B. bufo		**3**			**1**	**4**
Epidalea calamita			**1**			**1**
Rana temporaria	**1**			**2**		**3**
Anguis fragilis	**1**	**1**	**2**	**1**		**5**
Chalcides striatus	**1**		**1**	**1**		**3**
Lacerta* cf. *bilineata	**3**		**1**	**1**		**5**
Timon lepidus	**1**			**1**		**2**
Lacertidae indet. (small size)	**1**			**1**		**2**
Coronella austriaca	**2**		**1**			**3**
***Vipera* sp. (*aspis*/*seoanei*)**	**1**					**1**
Arvicolinae indet.	**3**	**1**	**3**	**1**	**1**	**9**
Microtus arvalis					**1**	**1**
Terricola duodecimcostatus			**2**			**2**
Apodemus sylvaticus	**1**			**1**		**2**
TOTAL (NMI)	**84**	**11**	**15**	**46**	**24**	**180**

Table 4.6.- Distribution of small vertebrates according to the minimum number of individuals (MNI) by pellets from MIR5, El Mirador cave.

and with heliophilous tendencies, with *C. striatus* as the dominant species, and to a lesser extent *E. calamita* and *A. fragilis* (MIR4-Q21-n227, MIR4-Q21-n228, MIR4-Q21-n231, MIR4-Q21-n233, MIR4-Q21-n234, MIR4-Q21-n235, MIR4-P21-n243, MIR4-Q21-n245 and MIR4-P22-n380). Finally, in more eccentric positions, two pellets (MIR4-Q21-n245 and MIR4-P21-n246) share the presence of *A. sylvaticus*, considered a marker of forest environments, in concurrence with a high number of arvicoline voles (*M. agrestis*, *M. arvalis* and *T. duodecimcostatus*) (Figure 4.4.B).

4.4.2.2. *MIR5*

The results for MIR5 are very different due to the exceptional predominance of *Hyla* gr. *H. arborea* over the rest of taxa and the relatively low number of pellets preserved at this level.

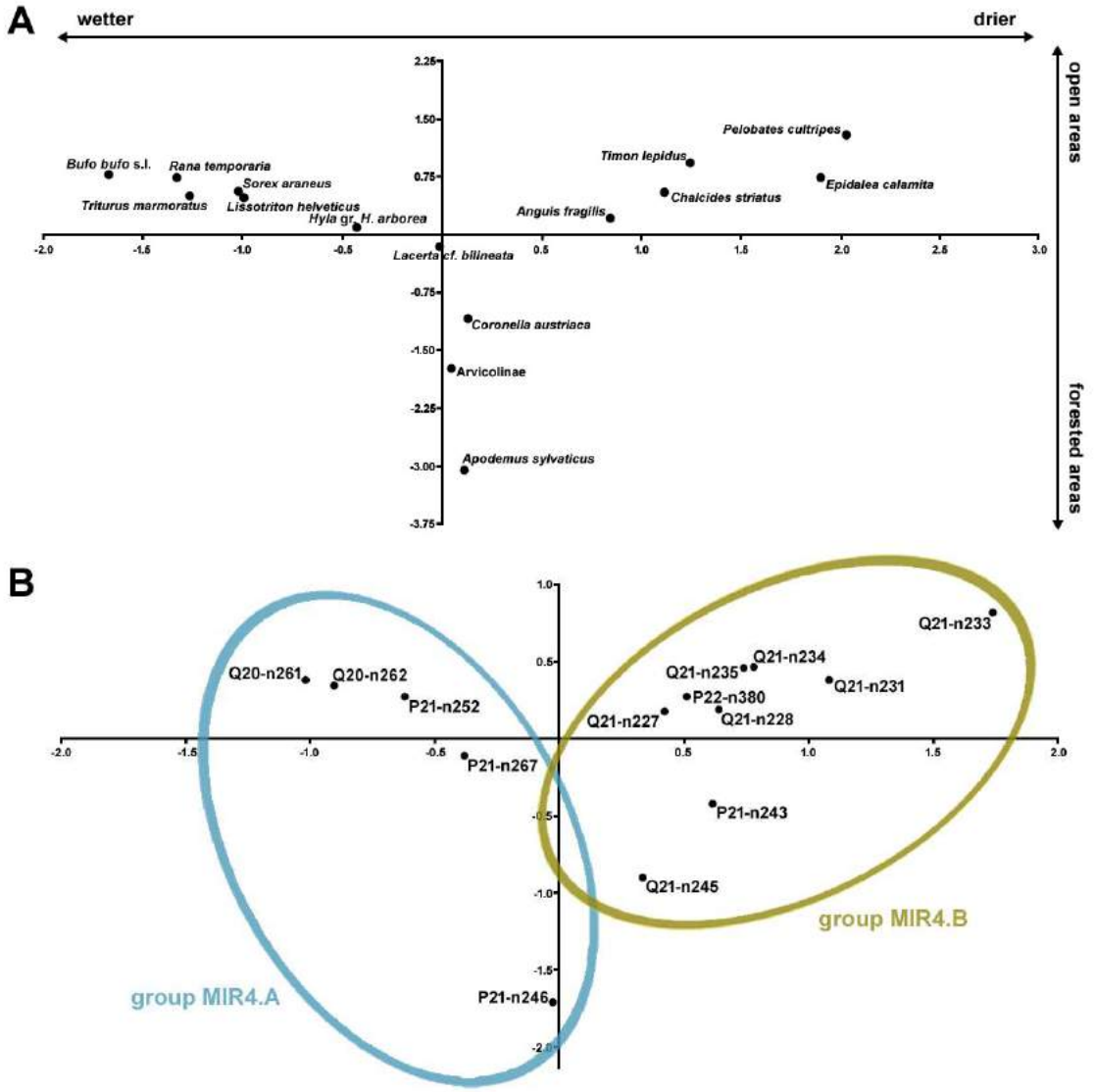

Figure 4.4.- Correspondence Analyses of the taxa (A) and pellets (B) from MIR4, El Mirador cave.

In the graphic, this appears as a large accumulation of the taxa in a group monopolised by *Hyla* gr. *H. arborea* that corresponds to pellets MIR5-P22-n2, MIR5-P21-n4 and MIR5-P21-n13, in which this tree frog represents between 71.74 to 87.50% of the MNI. The remaining taxa appear in more eccentric positions, determined by the concurrence of pellets MIR5-P21-1 and MIR5-P21-7, marked by *E. calamita* and *B. spinosus* together with *P. cultripes*, respectively (Figure 4.5.A and 4.5.B).

4.4.3. *Palaeoenvironmental reconstructions*

The habitat weighting method, both in MIR4 and MIR5, suggests a mostly open environment, primarily

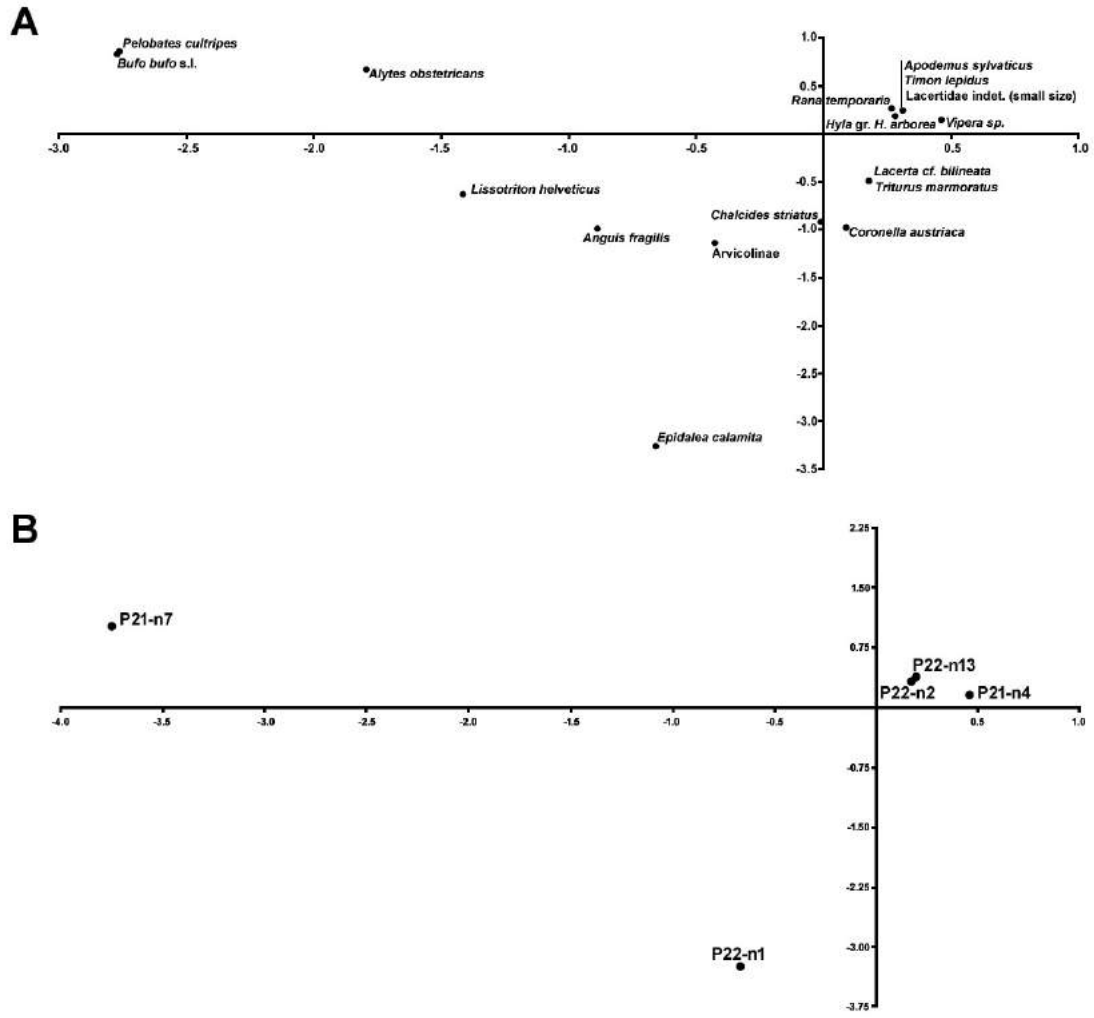

Figure 4.5.- Correspondence Analyses of the taxa (**A**) and pellets (**B**) from MIR5, El Mirador cave.

made up of open humid habitats (31.71–44.62%) and to a lesser extent rocky (9.02–10.82%) and open dry habitats (5.32–11.41%). The presence of woodland environments was also detected, which include medium scrublands to forest formations (23.79–26.29%), together with aquatic and peri-aquatic areas (25.86–26.04%), such as rivers or ponds with riverside vegetation (Figure 4.6). These habitat distribution percentages are consistent with the faunal composition identified and predominance of hygrophilous taxa over the comparatively more thermo-xerophilic.

Diachronically, the environmental differences detected between MIR4 and MIR5 are the increase in open dry areas (+2.21%), woodlands (+2.50%) and rocky habitats (+8.36%), and the decrease in open humid areas (-12.91%) (Figure 4.6). However, the representation of aquatic environment habitats in the two levels is quite similar (-0.18%). This is due primarily to the

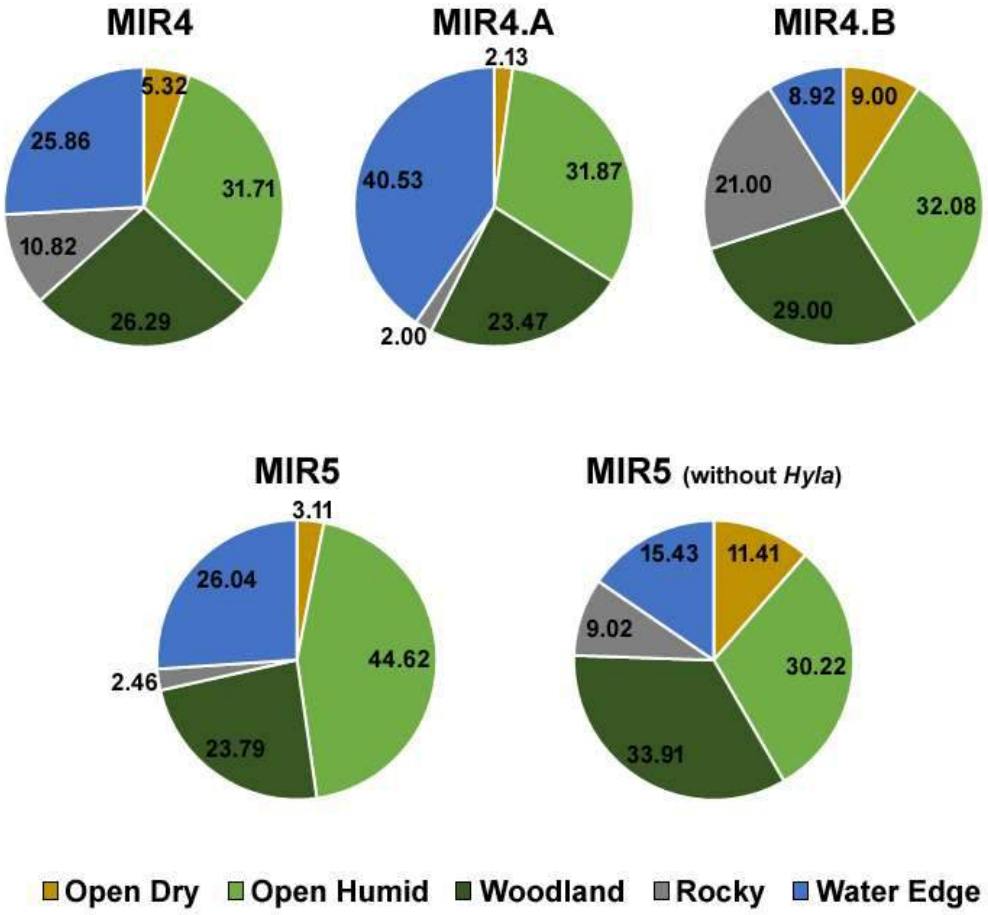

Figure 4.6.- Palaeoenvironmental reconstructions based on the Habitat Weighting method for MIR4 and MIR5 pellets, El Mirador cave. The values are in percentages (%).

over-representation of *Hyla* gr. *H. arborea* in MIR5 (66.33%), a typical anuran of wet environments and water pond areas, which is represented in much lower percentages in MIR4 (7.65%). Furthermore, MIR4 contains a higher representation of taxa typical of comparatively rockier and drier areas, such as *E. calamita* and *C. striatus*.

When statistically separating the pellets in MIR4 into two groups (Figure 4.4.A), the first group, MIR4.A, corresponds to the pellets indicating, through habitat weighting analyses, high percentages of open humid (31.87%) and aquatic environments (40.53%) and low percentages of open dry (2.13%) and rocky habitats (2.00%); whereas the situation is reversed in the second group (MIR4.B), with high percentages of open dry and rocky environments (30%) to the detriment of open wet and aquatic areas (41%). On the other hand, woodland environments are relatively similar in both groups (23.47–29%). Removing the over-represented *Hyla* gr. *H. arborea* results in a percentage increase in all habitats to the detriment of open humid environments, although the scenario is similar to previous ones (Figure 4.6).

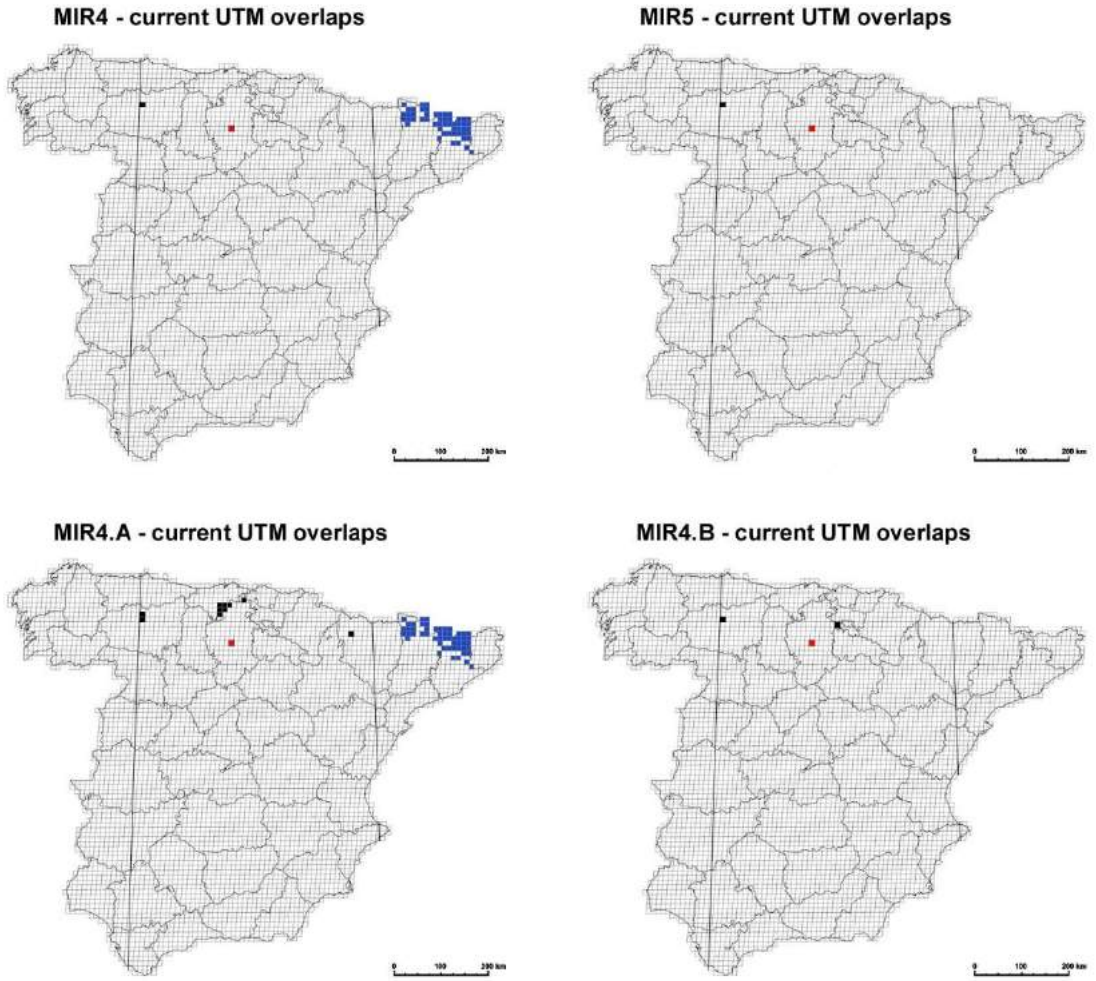

Figure 4.7.- 10x10 km UTM square overlaps of the herpetofaunal and small-mammal species present in the pellets from MIR4 and MIR5, El Mirador cave. In black the UTM squares used for MER, in red the location of Atapuerca, in blue the current distribution of the shrew *Sorex araneus*.

4.4.4. *Palaeoclimatic reconstructions*

4.4.4.1. *MIR4 vs. MIR5*

The geographical distributions of all species present in the pellets of MIR4 and MIR5 coincide in at least a 10x10 km UTM square, except in the case of *S. araneus* (MIR4 and MIRA.B). The shrew *S. araneus* is a species of Eurosiberian requirements that currently has a widespread geographical distribution covering most of western Eurasia, but is restricted to the eastern Pyrenees on the Iberian Peninsula and the northern Pyrenees in southwestern France, with no connection to other European populations (López-Fuster et al., 1999; Shchipanov and Pavlova, 2016). This isolation is attributed to the progressive retraction of its range due to the climatic warming of the Holocene and particularly to the increasing

Temperature (in °C)	MAT	J	F	M	A	M	J	J	A	S	O	N	D
Actual	**10.1**	**2.6**	**3.8**	**6.5**	**8.2**	**11.5**	**15.4**	**18.6**	**18.7**	**15.9**	**11**	**6.2**	**3.3**
MIR4	**9.8**	**2.3**	**3.7**	**6.3**	**8.0**	**11.2**	**15.4**	**17.9**	**17.9**	**15.1**	**10.5**	**6.0**	**3.2**
SD	-	-	-	-	-	-	-	-	-	-	-	-	-
MIR4.A	**10.5**	**3.8**	**4.7**	**7.1**	**8.6**	**11.6**	**15.3**	**17.8**	**17.9**	**15.6**	**11.5**	**7.4**	**4.9**
SD	1.1	1.6	1.3	1.3	1.1	0.9	0.7	0.6	0.7	0.9	1.2	1.4	1.6
MIR4.B	**11.1**	**3.9**	**5.2**	**7.8**	**9.3**	**12.5**	**16.3**	**18.8**	**18.9**	**16.4**	**12**	**7.4**	**4.8**
SD	1.8	2.3	2.1	2.1	1.8	1.8	1.3	1.3	1.4	1.8	2.1	2.0	2.2
MIR5	**9.8**	**2.3**	**3.7**	**6.3**	**8.0**	**11.2**	**15.4**	**17.9**	**17.9**	**15.1**	**10.5**	**6.0**	**3.2**
SD	-	-	-	-	-	-	-	-	-	-	-	-	-

Precipitation (in mm)	MAP	J	F	M	A	M	J	J	A	S	O	N	D
Actual	**594**	**50**	**46**	**44**	**57**	**64**	**50**	**30**	**31**	**47**	**51**	**63**	**61**
MIR4	**721**	**59**	**62**	**37**	**65**	**64**	**49**	**33**	**39**	**56**	**77**	**94**	**86**
SD	-	-	-	-	-	-	-	-	-	-	-	-	-
MIR4.A	**827**	**72**	**66**	**59**	**74**	**72**	**59**	**40**	**49**	**67**	**80**	**95**	**94**
SD	84.2	11.8	9.5	11.5	6.8	6	6.4	3.7	6	9.3	8.4	9.8	13.5
MIR4.B	**735**	**64**	**62**	**45**	**64**	**66**	**54**	**34**	**41**	**61**	**74**	**85**	**85**
SD	17.7	7.1	0.0	11.3	1.4	2.4	7.1	1.4	2.8	6.4	4.2	13.4	2.1
MIR5	**721**	**59**	**62**	**37**	**65**	**64**	**49**	**33**	**39**	**56**	**77**	**94**	**86**
SD	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 4.7.- Palaeoclimatic parameters according the overlaps obtained by Mutual Ecogeographic Range method through the faunal associations from the pellets of MIR4 and MIR5, El Mirador cave.

competitive pressure of *Sorex coronatus*, which has recently expanded from southwestern France (López-Fuster, 2007; Mackiewicz et al., 2017). The current geographical range of *S. araneus* on the Iberian Peninsula does not correspond to its potential range due to the mutual exclusion of *S. coronatus* (López-Fuster, 2007b). Therefore, *S. araneus* was removed from the analyses for MIR4 because its distribution is biased by a competing species. With this exclusion, the overlaps for both MIR5 and MIR4 are identical and correspond to a single UTM square (30T-TN63) in the northern León region (Figure 4.7).

The climate data obtained for MIR4 and MIR5 (Table 4.7) through the mutual ecogeographic range method suggest an MAT of 9.8 ºC, i.e. slightly lower than the current value (10.1 ºC), mainly due to lower mean temperatures during the summer months and early

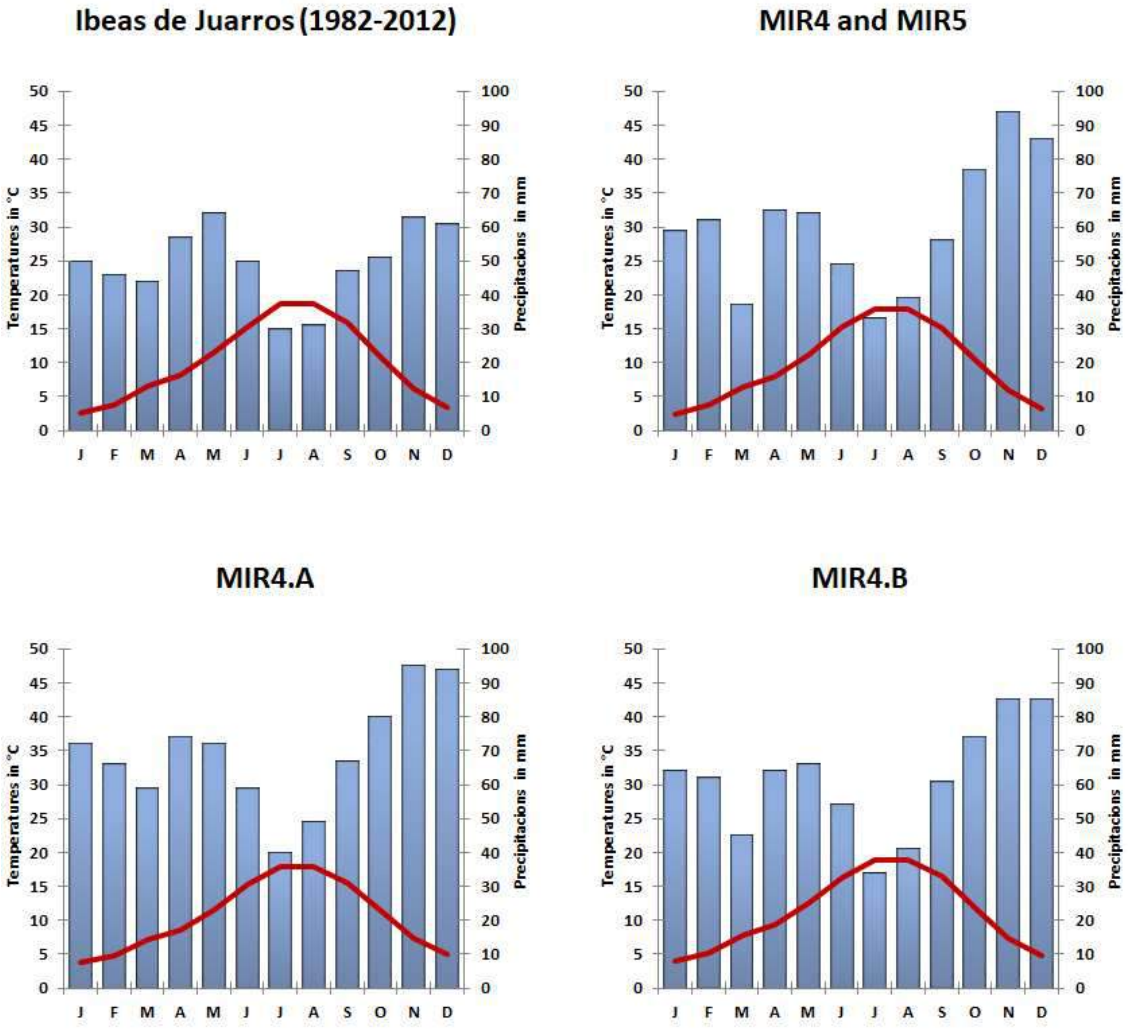

Figure 4.8.- Climographs of the palaeoclimatic parameters according the overlaps obtained by Mutual Ecogeographic Range method through the faunal associations from the pellets of MIR4 and MIR5, El Mirador cave.

autumn (between -0.7 ºC and -0.8 ºC from July to September) and slightly lower during the rest of the year (between -0.1 ºC and -0.5 ºC) (Table 4.7). The range of atmospheric temperature throughout the year was 15.6 ºC, between the warmest months (July and August, 17.9 ºC) and the coldest month (January, 2.3 ºC). In contrast, the differences in MAP are more significant, calculated at 721 mm for MIR5, 127 mm more than at present (594 mm). In general, the rainfall regime was regular, like today, but with higher rainfall after the summer. There was a dry period during July and August, with monthly rainfall of less than 40 mm. Precipitation increased during autumn and winter, reaching its peak in mid-autumn (94 mm) (Table 4.7).

4.4.4.2 *MIR4.A vs. MIR4.B*

The palaeoclimatic data for MIR4.A and MIR4.B were analysed to explore the effects that the groups identified by means of the correspondence analyses may have had on palaeoclimatic reconstructions. For MIR4.A, the number of overlaps in 10x10 km UTM squares is ten (30T-TN63, 30T-TN64, 30T-VN24, UT-VN25, 30T-VN26, UT-VN35, 30T-VN36, 30T-VN46, 30T-VN77 and 30T-XN90), because of the assemblage of Eurosiberian and generalist species. In MIR4.B, it was reduced to two squares (30T-TN63 and 30T-WN02) because of the assemblage of Eurosiberian and Mediterranean species (Figure 4.7).

An MAT of 10.5 ºC was obtained for MIR4.A and 11.1 ºC for MIR4.B, higher than both the current MAT and that estimated for MIR4. The mean monthly temperatures are higher for MIR4.A, especially during autumn and winter (Table 4.7 and Figure 4.8).

The MAP in MIR4.A is higher than in MIR4, with 827 mm (+106 mm), in spite of the same rainfall distribution throughout the year. The MAP in MIR4.B is similar to that of MIR4, 735 mm (+14 mm) (Table 4.7 and Figure 4.8). However, due to the low number of concurrences, the standard deviation is very high, mostly in the case of MIR4.B. MIR4 and MIR5 have no standard deviation because only one concurrence was obtained (Table 4.7).

4.5. Discussion

The comparative study of the nineteen small vertebrate accumulations of MIR4 and MIR5, interpreted as pellets or parts of pellets, suggests the existence of variations in the taxonomic composition and number of individuals, at least for MIR4. The pellets from MIR5, however, include a sample biased by the overabundance of *Hyla*. gr. *H. arborea*. Correspondence analyses have separated the MIR4 pellets into two different groups. The first group (MIR4.A) is primarily made up of amphibians, in which hydro-hygrophilous species with generalist and/or Eurosiberian requirements predominate. Reptiles and heliophilous species prevail in the second group (MIR4.B), but Mediterranean, Eurosiberian and generalist species are also associated with it. The palaeoenvironmental reconstruction points to a mostly humid environment, but with variations between higher humidity (MIR4.A and MIR5) to relatively drier conditions (MIR4.B). For all samples, the palaeoenvironmental data indicate a climate similar to today's, but with significantly more rainfall.

The peculiarities of this record and its interpretation in terms of seasonality are discussed below. The possible effects of biases that may be introduced in the paleoenvironmental and paleoclimatic reconstructions will also be examined.

4.5.1. *Seasonal selection and predation*

4.5.1.1. *Seasonality of the pellet depositions*

The faunal associations documented in MIR4 and MIR5 are characterised by their extraordinarily unique species assemblage. Excluding the case of *S. araneus*, the only UTM square on the Iberian Peninsula in which the same species of herpetofauna and micromammals are currently found is a small area on the southern slopes of the Cantabrian Mountains, in the region of León, where the Omaña highlands converge with the valley of the river Luna (Palomo et al., 2007; AHE, 2020) (Figure 4.7). This faunal association is very special due to the combined record of typically Mediterranean species, such as *T. lepidus*, with other typically Eurosiberian species, such as *R. temporaria*. Even more unusual is the concurrence of the anurans *P. cultripes* and *R. temporaria*, which in the northern Iberian Peninsula only occurs in seven 10x10 km UTM squares between Galicia and Navarra. In the northeast Iberian Peninsula, they concur in 24 UTM squares in northern and central Catalonia (AHE, 2020). The virtual line drawn by the above-mentioned squares coincides with the boundary between the two main macrobioclimates of the Iberian area: the Mediterranean macrobioclimate and the temperate macrobioclimate with an Atlantic-Eurosiberian influence (López Fernández et al., 2008). This pattern is consistent with the environmental and climatic requirements of the species documented in MIR4 and MIR5.

The correspondence analyses have shown the existence of two groups of pellets within MIR4 based on the presence of distinct species and differences in the number of individuals. This is not the case for MIR5, which is monopolised by *Hyla* gr. *H. arborea*. The comparison of the pellets from MIR4 by means of species concurrences and according to the ethology, phenology and annual activity of the species that currently inhabit the Burgos region (Diego-Rasilla and Ortiz-Santaliestra, 2009; Ortiz-Santaliestra et al., 2011) would identify both groups (MIR4.A and MIR4.B) as the product of two different seasonal periods, but contiguous in time.

The group dominated by newts, frogs and toads as opposed to squamates (58 amphibians vs. 10 squamates) (MIR4.A, comprising MIR4-P21-n246, MIR4-P21-n252, MIR4-Q20-n261, MIR4-Q20-n262 and MIR4-P21-n267) would suggest a period in the year with an abundance of active amphibians, possibly related to the beginning of the breeding season. The breeding season today on the Iberian Peninsula (or in northern Spain) begins with the early rainfalls at the end of winter or the beginning of spring, between February and March (García-París et al., 2004; Diego-Rasilla and Luengo, 2007; Diego-Rasilla and Ortiz-Santaliestra, 2009). Meanwhile, the group in which squamates predominate over amphibians (48 squamates vs. 18 amphibians) (MIR4.B, and comprising MIR4-Q21-n227, MIR4-Q21-n228, MIR4-Q21-n231, MIR4-Q21-n233, MIR4-Q21-n234, MIR4-Q21-n235, MIR4-P21-n243, MIR4-Q21-n245 and MIR4-P22-n380) suggests a

later period of the year, coinciding with the beginning of squamate activity brought about by the increasing temperatures and higher insolation starting in April and May and possibly extending to the summer (Ortiz-Santaliestra et al., 2011) (Figure 4.4.A). This is consistent with the presence in MIR4.B of thermophilic and Mediterranean species, such as *P. cultripes*, *E. calamita*, *T. lepidus* and *T. duodecimcostatus*, which are absent in MIR4.A. In addition, the presence of arvicoline voles in MIR4.A is consistent with a deposition event during the spring and summer months, when the peak activity of these rodents outside their underground burrows occurs due to the growth of vegetation cover after the winter recess (Brügger et al., 2010).

In contrast, the MIR5 pellets suggest another seasonal scenario, owing to the predominant presence of *Hyla* gr. *H. arborea* over all other taxa, as well as the relatively low number of pellets preserved in this level. MIR5 can be interpreted as part of a season-related assemblage, formed during a time when *Hyla* gr. *H. arborea* would have been found in great abundance in the areas surrounding cave. The most plausible scenario is that the deposition event occurred during the reproduction period of *Hyla molleri* (the endemic species of *Hyla* gr. *H. arborea*), i.e. between April and May, when large agglomerations of adult individuals congregate at water points (Lizana et al., 1989; Diego-Rasilla and Ortiz-Santaliestra, 2009), as also previously proposed for the largest pellet MIR5-P21-n4 (Chapter 3). The presence of thermophilic species in the MIR5 assemblage, which start their annual activity later than the generalist and Eurosiberian species, is consistent with the proposed period.

4.5.1.2. *Palaeoenvironmental reconstruction or habitat selection by the predator?*

The Holocene palynological record of El Mirador generally depicts a mosaic landscape made up of different plant communities comprising mixed forests of *Pinus* (pine), deciduous and evergreen *Quercus* (Portuguese oak, holm oak, common oak, etc.), *Corylus* (hazel), *Fagus* (beech) and *Juglans* (walnut tree), with swathes of *Cistus* or *Helianthemum* (rockrose) in the clearings formed in the interior, along with riparian communities or riparian forests of *Salix* (willow), *Tilia* (lime tree), *Ulmus* (elm) and *Alnus* (alder), accompanied by hydrophilic taxa such as Cyperaceae, *Typha-Sparganium* (reedmace-burreed) and *Myriophyllum* (watermilfoil) in rivers or other nearby water bodies. The surrounding grasslands were represented by Poaceae (grasses) and other grasses such as *Asphodelus* (asphodel), Asteraceae, Apiaceae, *Artemisia*, Chenopodiaceae, *Plantago* spp., Ranunculaceae and Urticaceae. The complex was intermittently accompanied by cereal crops (*Triticum aestivum*/*durum*, *Triticum dicoccum*) and other species related to livestock activities, which become increasingly distinct as the Holocene advances to the Bronze Age with the growing anthropisation of the

landscape (Rodríguez et al., 2016; Expósito et al., 2017).

Palynological studies of MIR4 and MIR5, however, show evidence of a possible increase in environmental aridity: the percentage of tree pollen from *Pinus* increases drastically, while riparian taxa, mesophilous plants and deciduous *Quercus* disappear or are minimally present in these levels. In turn, the taxonomic diversity of trees and shrubs decreases, including among taxa linked to anthropisation and livestock pressure (Expósito et al., 2017). These archaeobotanical data are very different from those yielded using the habitat weighting method to analyse the pellets, especially with regard to environmental aridity/humidity.

Although normally used for palaeoenvironmental reconstruction based on microvertebrate assemblages, habitat weighting results may also reflect in some way the accumulating agent's selection among the different available habitats around its nest. This is clearer in this case because our fossil assemblages come from non-dispersed pellets that have not mixed with other contributing agents, such as in situ mortality, etc. From this perspective, habitat variability in palaeoenvironmental reconstructions can be attributed to seasonal deposition for the different pellet groups. Based on seasonality, the habitat selection for MIR4 and MIR5 is interpreted within three different seasonal ranges (Figure 4.9):

- The pellets from MIR4.A, attributed to late winter-early spring, with a predominance of hydro-hygrophilous taxa, may suggest preferential habitat selection towards wet meadows and peri-aquatic environments. Rocky areas and dry open environments are not well documented.

- The pellets from MIR5, attributed to mid-spring in accordance with the timing of the reproduction period of tree frog *Hyla* gr. *H. arborea* (*H. molleri*). The habitat selection is similar to MIR4.A pellets, towards open humid and water habitats.

- The pellets from MIR4.B, attributed to late spring and/or summer, made up mainly of heliophilous species associated with open habitats and Mediterranean and thermophilic species. The habitat selection results show an increase in open dry environments and rocky habitats and a decrease in wet grasslands and peri-aquatic environments, although humid habitats are still the predator's primary habitat selection.

From an environmental point of view, the changes in the percentages of representation in habitat selection by the predators in MIR4 and MIR5 are consistent with the evolution of plant communities and environmental humidity during the period between late winter and summer, with a dryness beginning in late spring that reaches its maximum in summer (García-Mijangos, 1997; Alejandre et al., 2006; Loidi et al., 2011). Accumulated precipitation during the winter and low temperatures cause high environmental humidity that is maintained as a result of the rainfall between April and May, despite higher springtime temperatures. After this

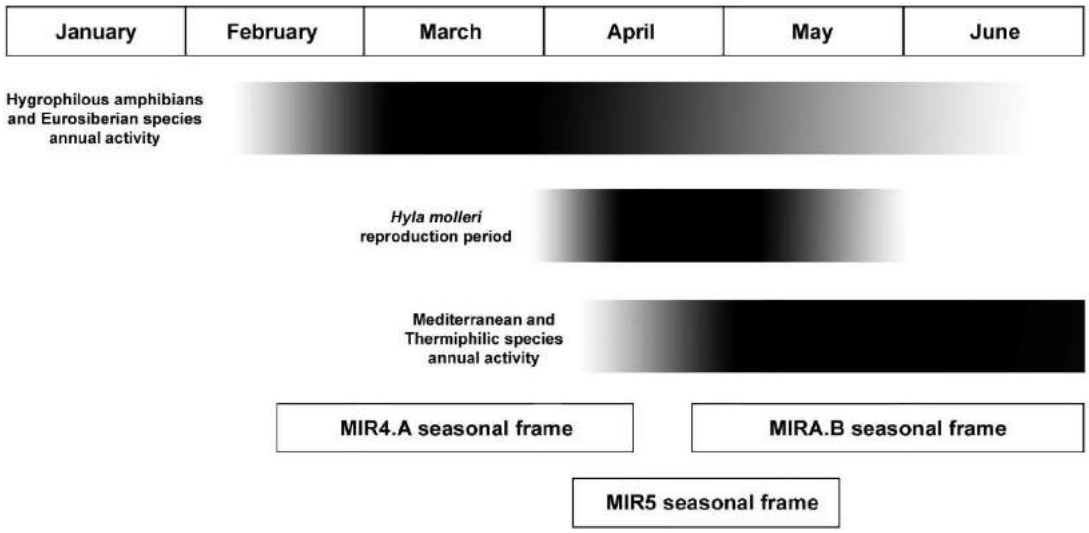

Figure 4.9.- Proposed seasonal periods for the pellets from MIR4 and MIR5, El Mirador cave.

period, aridity increases due to the decrease in summer rainfall and higher atmospheric temperatures, which gives rise to greater evaporation (Table 4.7 and Figure 4.8). This also correlates with the reproductive cycles of the herpetofauna, especially amphibians that require an aquatic larval phase (García-Paris, 2004), because they are associated with conditions of continued environmental humidity and the existence of water sources. MIR4.A exhibits the highest percentages of habitats directly associated with high humidity, wet meadows and peri-aquatic environments. In contrast, in MIR4.B the drier environments increase in percentage, with more open dry and rocky habitats at the expense of the wet habitat. The percentages in MIR5, despite coming from an older level, are consistent with the scenario proposed in MIR4. The seasonality in MIR5 can be interpreted as an intermediate phase between MIR4.A and MIR4.B, a wet spring period prior to the increase in environmental dryness.

The predators' habitat selection suggests the existence of a varied environment around the cave for MIR4 and MIR5, which is mostly consistent with the archaeobotanical data for the Holocene sequence of El Mirador, but with considerable differences concerning aridity (Allué and Euba, 2008; Vergès et al., 2016; Rodríguez et al., 2016; Expósito et al., 2017). Palynological studies of levels MIR4 and MIR5, however, point to a possible increase in environmental aridity: the percentage of *Pinus* tree pollen increases drastically, while riparian taxa, mesophilous plants and deciduous *Quercus* disappear or are only minimally present in these levels. In turn, the taxonomic diversity of trees and shrubs decreases, including those taxa linked to anthropisation and livestock pressure (Expósito et al., 2017).

	MIR4				MIR5		
Habitats	**Small-Mammals**	**Pellets**	**Pellets MIR4.A**	**Pellets MIR4.B**	**Small-Mammals**	**Pellets**	**Pellets (without *Hyla*)**
Open Dry (%)	20.80	5.32	2.13	9.00	14.60	3.11	11.41
Open Humid (%)	19.80	31.71	31.87	32.08	30.90	44.62	30.22
Woodland (%)	59.40	26.29	23.47	29.00	54.50	23.79	33.91
Rocky (%)	0	10.82	2.00	21.00	0	2.46	9.02
Water Edge (%)	0	25.86	40,53	8.92	0	26.04	15.43

	Current	MIR4				MIR5	
Climate	**Ibeas de Juarros**	**Small-Mammals**	**Pellets**	**Pellets MIR4.A**	**Pellets MIR4.B**	**Small-Mammals**	**Pellets**
MAT (in ºC)	10.1	9.94	9.8	10.5	11.1	10.03	9.8
SD		1.5	-	1.1	1.8	1.6	-
MTC (in ºC)	2.6	2.54	2.3	3.8	3.9	2.65	2.3
SD		1.2	-	1.6	2.3	1.2	-
MTW (in ºC)	18.7	18.53	17.9	17.9	18.9	18.60	17.9
SD		1.4	-	0.7	1.4	1.4	-
MAP (in mm)	594	794	721	826	806	846	721
SD		221	-	84.2	17.7	284	-

Table 4.8.- Comparative between habitat and climatic data from small-vertebrate records (small-mammals according Bañuls-Cardona et al, 2017a).

This phenomenon of the predominance of *Pinus* among the tree pollen evidence together with its substitution by the evergreen *Quercus* is a generally observed throughout the Iberian Peninsula and is associated with increased human impact on plant communities (Carrión et al., 2010). Similar data suggesting a relationship between increased aridity in vegetation and greater anthropisation of the landscape have come from other regions of the western Mediterranean (Magny et al., 2002; Pérez-Díaz et al., 2016; Ramos-Román et al., 2018; Moreno-de las Heras et al., 2018). The palynological record points to an arid phase in the El Mirador sequence for level MIR5 and the bottom of MIR4, with a chronological interval between 5,300–3540 cal BP (Expósito et al., 2017) and is linked, at least in the El Mirador sequence, to the regional equivalent of the 4.2 ka event (4,100–3,950 cal BP) (Magny et al., 2002, 2009).

4.5.1.3. *Predator diet and human impact*

The diet of the predators in the MIR4 and MIR5 pellets clearly displays a preference for herpetofauna species. The main groups represented in the pellets

are amphibians (MIR4: 40.13%; MIR5: 80.55%), with some reptiles (MIR4: 38.85%; MIR5: 11.67%) and small mammals (MIR4: 19.75%; MIR5: 7.78%) in the background, along with the testimonial presence of birds in MIR4 (1.27%).

The published studies on the diet of the two species proposed as possible sources of the accumulation, the eagle-owl *B. bubo* (Hiraldo et al., 1975; Pérez-Mellado, 1978; Vericad et al., 1976; Andrews, 1990; Mikkola, 1995; Serrano, 1998; Sándor and Ionescu, 2009; Obuch and Karaska, 2010; Penteriani and Delgado, 2016) and tawny owl *S. aluco* (Uttendörfer, 1952; Nores, 1980; Alegre et al., 1989; Mikkola, 1995; Villarán, 2000; Romanowsky and Żmihorski, 2009) indicate that their diets mainly comprise mammals, and birds and/or insects, with little or very little herpetofauna. However, amphibians may occasionally represent more than 40% of preys, especially in European populations of *B. bubo* (Hagen, 1950; Frey and Walter, 1986). The maximum percentage of amphibians among the preys of *S. aluco* is lower, with exceptional highs approaching 10% (Uttendörfer, 1952; Mikkola, 1995; Romanowsky and Żmihorski, 2009). The presence of amphibians in the pellets of El Mirador exceeds these percentages with very high values, 40.13% in MIR4 and 80.55% in MIR5. What is more unusual is the high presence of reptiles, which reach a maximum of 38.85% in MIR4 and a lower percentage in MIR5 of 11.67% due to the high percentage of *Hyla* gr. *H. arborea* in the pellets from this level. In the literature, the maximum percentage of reptiles among *B. bubo* preys is 28% in eastern Europe (Penteriani and Delgado, 2019). This high representation of reptiles, mostly diurnal species, led us to postulate that *B. bubo* was the accumulating agent of these pellets, as it is a mostly nocturnal and crepuscular species that is also active during the day, unlike *S. aluco* which is much more exclusively nocturnal (Mikkola 1995; Sunde et al., 2003; Penteriani and Delgado, 2019).

The existence of seasonal variation in diet has been unequivocally documented in nocturnal raptors on the Iberian Peninsula, including the eagle-owl (Pérez-Mellado, 1978; Zerunian et al., 1982; Donázar, 1989; Lara, 1995; García and Cervera, 2001; Andrews and Fernández-Jalvo, 2018). Studies on the composition of the *B. bubo* diet in northern Slovakia have found seasonal predation preferences during spring for the rodents *M. arvalis* and *Arvicola amphibius* and for the frog *R. temporaria*, following the annual cycles of these preys (Obuch and Karaska, 2010). This same study also states that the high representation of frogs (27.90%) and small rodents (51.10%) is due to the growing anthropogenic impact in the prospected area in recent decades consisting of the expansion of extensive agriculture to the detriment of forests, which has decreased biodiversity and the spectrum of available preys for *B. bubo* (Obuch and Karaska, 2010). This phenomenon has been observed in other raptors, such as *Tyto alba* (barn owl), which showed changes in the composition of its diet between 1974 and 1994 in Great Britain: a decrease in the

abundance and diversity of its prey and an increase in its dependence on a lower number of species – changes that were associated with new agricultural practices (Love et al., 2000).

In the Mediterranean region, there is also evidence of changes in the diet of the eagle-owl caused by anthropogenic impacts. In Wadi Al Makhrour (Palestine), an increase in population of the invasive black rat *Rattus rattus* to the detriment of native species was linked to the growing anthropisation of the landscape (massive urbanisation) and to the adaptation of the diet of the eagle-owl for new environments, with low biodiversity and variety of preys (Amr et al., 2016). In the Middle Valley of the Ebro River (north-eastern Spain), *B. bubo* presents regional differences in its diet associated with the presence of the European rabbit *Oryctolagus cuniculus*: a reduced number of rabbits correlates with a higher diversity of preys (Serrano, 1998). The same study links the regional rarity of *O. cuniculus* with rabbit haemorrhagic disease (RHD), an infectious disease caused by the calicivirus *Lagovirus* and spread by humans worldwide (Abrantes et al., 2012). This can therefore be considered another human impact.

As mentioned earlier, the palaeoclimatic and palaeoenvironmental conditions suggested by the archaeobotanical remains for MIR4 and MIR5 diverge from the results yielded by the analysis of the pellet groups. The disappearance of plant species associated with water and wet environments contrasts with the high representation of aquatic and semi-aquatic amphibians and with the humid habitats that the accumulating agent would have selected, as well as with the higher reconstructed rainfall for both levels. Although the scale is different, the content of pellets can record the environmental conditions around the cave (2.3 km² for an adult B. bubo), while pollen analyses document changes undergone at a macro/regional level. Therefore, it is possible that the two dynamics are related, and not opposing. Palynological and anthracological studies have pointed to increasing anthropogenic impact on the landscape around the cave from the bottom to the top of the sequence, reaching a maximum in MIR5 and at the base of MIR4 (Allué and Euba, 2008; Expósito et al., 2017). The eagle-owl *B. bubo*, the potential accumulating agent of the pellets from El Mirador, is known to be a generalist predator that is highly adaptable to environmental alterations and able to modify its diet to adjust to anthropogenic changes in the landscape (Obuch and Karaska, 2010; Abrantes et al., 2012; Amr et al., 2016; Penteriani and Delgado, 2019). Therefore, the human impact on the landscape is a plausible hypothesis to explain the differences observed between the palaeobotanical data and the exceptional diet of the predator.

As referred to earlier, adult eagle-owls have an average vital territory of 2.3 km² around their nests (Penteriani et al., 2015). Applied to the El Mirador cave, this would cover the southern part of the Sierra de Atapuerca and the river terraces formed by the Chorruela brook in its southern part (Figure 4.10). Outside of this theoretical radius, but nevertheless

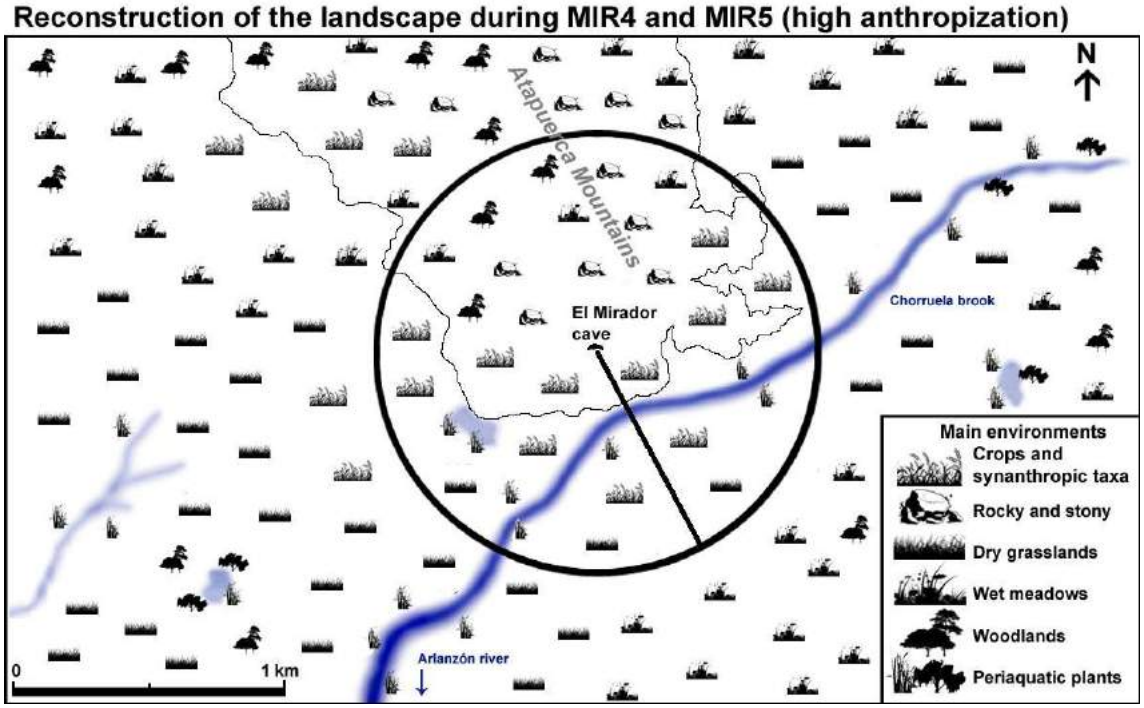

Figure 4.10.- Hypothetical reconstruction of the Atapuerca's landscape during the Chalcolithic and Early Bronze Age. The circumference represents the average vital territory of an adult eagle-owl *Bubo bubo* (Penteriani et al., 2015).

very nearby, there is the cave of Portalón de Cueva Mayor, the other main human habitat site in Sierra de Atapuerca during the Holocene, which was also inhabited during the Chalcolithic and Bronze Ages (Carretero et al., 2008). During the Chalcolithic and Early Bronze Age, El Mirador was used as a burial site (Vergès et al., 2016), which would have made it possible for owls to settle inside the cave in an environment undisturbed by human activities. In contrast, pronounced human impact on the surrounding territory could explain the predator's exceptional diet, which has no parallel in the contemporary literature on European birds of prey. Anthropisation gave rise to the degradation of plant communities in the owl's hunting area and possibly to a decrease in available prey (such as rabbits). There is evidence of human consumption of *Oryctolagus cuniculus* at El Mirador, before and after the deposition of the pellets, including evidence of human consumption of carnivorous mammals: foxes, wild cats and badgers (Martín et al., 2014). The owl would have preyed on amphibians and reptiles, an abundant resource in the environment but outside the food interest of local human communities. This predilection would generate discordance between the predominant habitat documented by the content of the pellets and the archaeobotanical data, since the predator would have focused on the wet areas where its alternative prey congregated due to its vital requirements: water points and wet meadows.

Despite the results of palynological analyses, the continued presence of wet habitats around the cave as suggested by the composition of the pellets is supported by anthracological data from El Mirador. In addition to the burnt coals recovered from MIR4 that point to a degradation of the forest cover due to the increased variability of shrub taxa, the presence of deciduous *Quercus*, *Fraxinus* (ash plant) and *Sambucus* (elderberry) suggest the presence of humid environments (Allué and Euba, 2008; Rodríguez et al., 2016). Moreover, *Cornus* (dogwood), *Corylus avellana* (common hazel), *Fagus sylvatica* (European beech) and *Salix* (willow) have been found at the base of MIR4, in the same stratigraphic horizon as the pellets (Allué and Euba, 2008; Cabanes et al., 2009). Whilst some of the plant material may have originated from a region distant from the cave and not from the surrounding area, the presence of these plants is associated with humid environments and/or temperate climates and is consistent with the palaeoclimatic data (Table 4.7 and Figure 4.8).

Approximately 5,000 years ago, in the Late Neolithic and Chalcolithic periods, the North Castilian Plateau and the Duero Valley were mainly inhabited by small groups of farmers with cereal agriculture and transhumant livestock, which cultivated the river terraces assisted by draught animals (Fabián, 2006; Carmona-Ballestero, 2013, 2014; Carmona-Ballestero et al., 2013; Delibes de Castro et al., 2015; Blanco-González et al., 2018). These characteristics are reproduced in El Mirador, where a mixed economy of agriculture and livestock has been documented, presumably carried out on the set of river terraces formed by the river Arlanzón and its tributary brooks to the south of the cave (Vergès et al., 2018). Even at El Mirador some evidence points to the use of bovines as work animals, as documented by the presence of osteopathologies associated with traction in MIR4 (Martín, 2015). Anthropogenic impact is also evident in the pollen sequences of the northern Meseta and other areas near the Sierra de Atapuerca. For example, a sequence from Espinosa de Cerrato (Palencia) shows two major landscape changes of anthropogenic origin: the first dated at c. 4,500 BP, with a decrease in the evergreen *Quercus* forests, followed by another between c. 3,000 and 2,000 BP affecting the *Pinus* forests. The change ends at c. 1,500 BP, when the remaining coniferous forests were replaced by a mostly shrub and cereal crop landscape (Franco et al., 2001).

To the east of Atapuerca, in the northern mountains of the Iberian System (Sierra de la Demanda, Sierra de Neila and Sierra de Urbión), palynological data reveal a correlation between prehistoric grazing in these high mountain areas and the expansion of the *Fagus* forests that occurred from c. 5,900 to 4,200 cal BP, which made possible their spread as a result of the opening up of new spaces (López-Merino et al., 2008). Likewise, this increase in *Fagus* was concurrent with the percentage increase in the presence of *Betula*, Ericaceae and other anthropogenic indicators that benefitted from previous deforestation (López-Merino et al., 2008). The increase in the anthropogenic

impact on the landscape in the northern Atlantic-Cantabrian boundary occurred later. In the nearby pollen sequence of Zalama (Basque Country), anthropogenic impact also occurred later (from c. 3,400 BP) and resulted in an increase in *Fagus* to the detriment of *Corylus* and deciduous *Quercus*, and the appearance of taxa associated with fire and overgrazing such as *Chaetomium* sp. and *Asphodelus albus* (Pérez-Díaz et al., 2016). All these data testify to the capacity of human communities to alter the landscape through anthropisation, generating changes in the record of the past, regardless of the climatic context.

Finally, the hypothesis of greater anthropisation of the landscape around El Mirador is consistent with the evidence provided by the small mammal remains (Bañuls-Cardona and López-García, 2016; Bañuls-Cardona et al., 2013, 2017a, 2017b). The small-mammal assemblages of MIR4 and MIR5 are made up of the insectivores *Crocidura russula* and *Sorex araneus-coronatus*, and by the rodents *M. arvalis*, *M. agrestis*, *T. duodecimcostatus* and *A. sylvaticus* (Bañuls-Cardona et al., 2017a, 2017b). The main difference between the two assemblages is the presence of *Eliomys quercinus* in MIR4, which is absent in MIR5 (Bañuls-Cardona et al., 2013, 2017a). These assemblages suggest an increase in open spaces to the detriment of forested areas during the transition from the Chalcolithic to the Bronze Age, without significant changes in precipitation or temperature. In contrast, the percentage of synanthropic species (benefitted by human activities: *C. russula*, *M. arvalis*, *T. duodecimcostatus* and *E. quercinus*) is high in both levels and in MIR4 it reaches the highest value in the entire sequence (Bañuls-Cardona et al., 2017b). In parallel, MIR4 has yielded evidence of increased open dry environments, which also reach their peak in the level, and a slight increase in wooded areas, although the growth of both of these types of environments resulted in diminished wet meadows in comparison with MIR5 (Bañuls-Cardona et al., 2017a).

The authors link these data to the increasing anthropisation of the landscape, which would have reached its peak during the Bronze Age, as represented by MIR4 (Bañuls-Cardona et al., 2017a, 2017b). Therefore, increased human impact that would have led to the degradation of plant communities can be successfully synchronised with palynological and anthracological data. All these proxies support the hypothesis that the high degree of human impact on the landscape and its effect on environments and preys are a plausible cause for the singular diet of the predators.

4.5.2. *Seasonality and palaeoenvironmental biases*

The hypothesis that the samples taken from the pellets recovered in MIR4 and MIR5 were affected by seasonality opens up the discussion about the possible biases that may occur in palaeoclimatic and palaeoenvironmental reconstructions undertaken using the MER and habitat weighting methods. The exceptional conditions inside the El Mirador cave during the burial phases of the Chalcolithic and the Bronze Age

allowed the pellets to be preserved intact (Vergès et al., 2002, 2016). These very unusual and relatively recent coprocoenotic accumulations in much more common conditions would have disintegrated in the sediment along with the microfaunal remains contributed by other sources, such as *in situ* mortality. Therefore, the possible seasonal effects would have been weakened by the rest of the small-vertebrate sample, minimising the biases produced in the palaeoenvironmental and palaeoclimatic reconstructions.

El Mirador has provided an interesting record of small mammals that has been used in both palaeoclimatic and palaeoenvironmental studies (Bañuls-Cardona et al., 2017a, 2017b), which serve as a reference and a point of discussion in relation to the data provided by the pellets (Table 4.8). Nevertheless, various clarifications should be made before comparing the two records.

The first difference between them is the time frame. The pellets were generated in predation events of few hours, at most days, while the associations of small mammals come from the entire archaeological level, which in MIR4 encompasses a minimum range of 140 years (between 3,530 to 3,390 cal BP) and a maximum of 660 years (between 3,730 to 3,070 cal BP), according to calibrated radiocarbon data (Vergès et al., 2016).

A second difference is that the comparison of associations made up exclusively of small mammals with grouped taphocenoses of mainly herpetofauna (78.98% in MIR4 and 92.22% in MIR5) may affect interpretation due to the physiological and ethological differences between the two samples, mainly endothermia versus ectothermia. A third point is the possible contribution to the sedimentary record from other sources, as referred to above.

Despite the differences between the two records, both the small mammals and the pellets indicate the existence of a climate similar to the present one, with the exception of the higher rainfall. The differences in temperatures are within the standard deviation, and are therefore not significant. However, the divergences between the data provided by the two microfauna samples are pronounced in the palaeoenvironmental records. Among the small mammals, representatives of shrub and forest environments predominate, whereas rocky and periaquatic environments are absent. In MIR5, evidence of wet meadow environments doubles in percentage compared to that of dry open areas, but in MIR4 the percentages of both habitats are equal. On the other hand, the content of the pellets testify to a mostly open and humid landscape, with abundant water points, wooded areas and, to a much lesser extent, rocky areas (Table 4.8).

The comparison between the small-mammal and the pellet assemblages is much more complicated, as pellets have a much more pronounced bias because they are directly associated with the selection of the predator, while the associations of small mammals could be contributed to the sedimentary record of the cave by a variety of sources, from different predators to in situ natural mortality. Taphonomic marks within the

small-mammal associations indicate that their remains were contributed by a category 1 predator (Bañuls-Cardona et al., 2017a), such as *Asio otus* (long-eared owl) or *T. alba*, opportunistic predators that prefer semi-forested and open areas (Bañuls-Cardona et al., 2017b). The participation of different coprocoenotic agents can explain the great variation in the environmental data of the two samples. A predator more linked to forest environments would have mostly contributed to the associations of small mammals in MIR4 and MIR5, dominated by *A. sylvaticus*, a species closely linked to forest habitats (Bañuls-Cardona et al., 2017a). Meanwhile, taphonomic analyses link the pellets to *B. bubo* (Chapter 3), more eclectic in its environmental preferences as a generalist predator (Hagen, 1950; Hiraldo et al., 1975; Pérez-Mellado, 1978; Vericad et al., 1976; Frey and Walter, 1986; Serrano, 1998; Penteriani and Delgado, 2016).

To conclude, the location of El Mirador de Atapuerca, on the biogeographical border between the Mediterranean and Eurosiberian regions of influence, makes it a place of special interest to monitor the changes associated with the 4.2 ka BP event. The archaeobotanical data coincide with the scenario proposed for the southern regions, with a marked increase in aridity (Allué and Euba, 2008; Rodríguez et al., 2016; Expósito et al., 2017). On the other hand, the record of the vertebrate microfauna suggests a scenario typical of the northern regions, with a continuance of the humid conditions in the environment. In the small-mammal sample, MIR5 is the sequence level with the highest percentage of species with Eurosiberian requirements (64%) (Bañuls-Cardona et al., 2017b), while in MIR4 they represent the second highest set in the association (36.5%).

Among the herpetofauna, the presence of the common brown frog *R. temporaria* in the pellets of MIR4 and MIR5 is diagnostic of Eurosiberian climatic and environmental conditions. This frog is highly conditioned by temperature, environmental humidity and rainfall (Álvarez, 2014), so it is highly susceptible to be negatively affected by aridity crises. This species is currently absent from the Sierra de Atapuerca and its closest populations are located 60 kilometres to the north and northeast, already within the Eurosiberian bio-region (Diego-Rasilla and Ortiz-Santaliestra, 2009, AHE, 2020; own data).

The distribution retraction of *S. araneus*, another typically Eurosiberian species present in MIR4, is even more extreme, as nowadays its Iberian populations are limited to the eastern Pyrenees (López-Fuster, 2007a, 2007b). The presence of both species between 4,530 cal BP to 3,530 cal BP means that environmental humidity was high during the 4.2 ka BP event and that locally there was no significant increment in aridity. This data also adds to the already compelling arguments for human impact as the primary factor in the degradation of the vegetation communities observed from archaeobotany in the latest sequence of El Mirador.

4.6. Conclusions

The comparative study of the accumulations of MIR4 and MIR5, interpreted as pellets or parts of them, suggests the existence of seasonal variations in the dietary composition of the accumulating agent. Through the ethology, phenology, annual activity and reproductive cycles of the documented preys, the existence of a determining seasonal factor is postulated. The MIR4 pellets point to a double seasonality, represented by the two groups separated by correspondence analyses. The MIR.A group is mainly composed of amphibians with a reproductive cycle and increased activity after hibernation and during the first weeks of spring. The second group, MIR4.B, is made up mainly of reptiles and species of more Mediterranean influence compared to the other group. For this reason, MIR4.B is situated in a period between mid-spring and summer, when reptiles reproduce and when the most thermophilic species begin their annual activity. In contrast, MIR5 is monopolised by *Hyla* gr. *H. arborea* (*H. molleri*), which reproduces massively in large agglomerations during the mid-spring wet phase.

The taxonomic composition and number of preys in the pellets from MIR4 and MIR5 are very unusual and have no parallel in contemporary literature. Modern data also suggest that human impact may cause changes in the diets of nocturnal raptors, as an adaptation to pressure from anthropogenic changes. Archaeobotanical data and the small-mammal record support the hypothesis of human impact as a conditioning factor for the predator in the Sierra de Atapuerca environment. Possibly in the absence or scarcity of more optimal preys, the predator (potentially *B. bubo* according to previous taphonomic data) opted for other less optimal but more abundant prey available in the surroundings, especially during their reproductive phases in accordance with seasonal cycles.

The palaeoenvironmental reconstruction through the different seasonal associations suggests changes in the distribution of the main habitats, with increased wet areas between late winter and mid-spring, and increased dryness between mid-spring and summer. The palaeoclimatic reconstruction points to a climate very similar to today's, albeit slightly wetter. The separated calculations according to seasonal criteria did not show significant differences in annual or monthly temperatures, although there were increases in precipitation from the associations assigned to winter through mid-spring. The comparison with the small-mammal record of MIR4 and MIR5 shows a high degree of coincidence with the palaeoclimatic reconstruction but greater discrepancies with the palaeoenvironmental interpretation. Although the record of pellets from El Mirador is exceptional in comparison with the usual scenario in karst sites, the new data provided in this research suggest the combined use of vertebrate macrofaunal associations for a higher degree of confidence in our reconstructions and interpretations of the past.

Supplementary data

Appendix 4.- Systematic description of the herpetofaunal remains from El Mirador pellets (MIR4 and MIR5) (pages 215-231).

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BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Chapter 5

Palaeobiogeographic analysis of the amphibians and reptiles from the mid-late Holocene transition (MIR4 and MIR5) of El Mirador cave (Atapuerca, Spain) in the north-Iberian post-glacial context

Abstract

The herpetofaunal associations from the pellets of MIR4 and MIR5 have reported a unique combination of species. Their compositions are a mixture of generalist and Eurosiberian taxa, hygrophilous and Mediterranean thermophilic species, which currently only occur in three 10x10 km UTM squares of the Iberian Peninsula. In this chapter we will study the peculiarities of these associations in the palaeobiogeographic context of the herpetofauna during the Late Quaternary. The location of the Sierra de Atapuerca, between the basins of the rivers Ebro and Duero and also situated between the Cantabrian Mountains and the Iberian Mountain System, makes it a reference point for understanding the changes in the distribution of species in the northern Iberian Peninsula. For this purpose, a statistical analysis of the herpetological occurrences of the last 60,000 years from northern archaeo-palaeontological sites will be carried out, including the new associations provided by El Mirador. The inclusion of the herpetofaunal associations of the pellets of MIR4 and MIR5 in the context of the north of the Iberian Peninsula during the Late Quaternary has shown their link with the process of post-glacial colonization of the north of the Iberian Peninsula by Mediterranean/thermophile species from the southern regions, as well as the survival of species from colder climates and environments in areas that are currently Mediterranean The geographical location of the Sierra de Atapuerca, in a natural corridor, would have made possible the arrival of species of multiple biogeographical origins during the Holocene.

5.1. Introduction

The most significant changes in the composition of the herpetofauna during the Late Quaternary occurred in the northern Iberian Peninsula (Chapter 1). During MIS 3 (ca. 60,000 to 26,900 BP) and MIS 2 (ca. 26,900 to 14,900 BP), the associations of amphibians and reptiles were made up solely of Eurosiberian or generalist species tolerant of cold conditions (Chapter 1). The main biogeographic changes occurred after the beginning of the postglacial phase (MIS 1, ca. 14,900 to present), with the resulting improvements in climate that led to the expansion of the thermophilic Mediterranean species towards the north of the Iberian Peninsula, possibly taking advantage of the existence of natural corridors. In parallel, newcomer taxa

entered the Iberian Peninsula via the Pyrenean boundaries.

In El Mirador cave (Burgos, Spain), twenty concentrated accumulations containing microfaunal remains with a significant abundance of herpetofauna were recovered from levels MIR4 and MIR5 (Figure 3.1), dated to the Chalcolithic to the Bronze Ages (Vergès et al., 2016). To determine their origin, a taphonomic analysis was performed on the larger accumulation (MIR5-P21-n4). The results identified it as a bird pellet produced by a category 2 predator, possibly the owls *Bubo bubo* or *Strix aluco*, which was preserved intact due to the special conditions of the cave during the Chalcolithic period, when it was used as a burial space (Chapter 3). Additionally, the quantitative taxonomic composition of this pellet indicates the seasonal predation of *Hyla* gr. *Hyla arborea* (*Hyla molleri*), during a period of abundance of this tree frog in the landscape around the cave, which would have been characterised by humid and temperate conditions (Chapters 3 and 4).

The individualised preservation of multiple accumulations interpreted as owl pellets from El Mirador cave containing great taxonomic variety (at least 20 different taxa of amphibians, squamate reptiles, birds and mammals) and a large number of individuals (350 MNI) has occasioned an approach to the problem of representation bias in a coprocoenotic record and its effects on palaeoenvironmental and palaeoclimatic reconstructions. The comparative study of the pellets using statistical methods showed the existence of variations in the presence and the number of individuals of the preyed species. These differences have been interpreted as seasonal variations in the predator's diet in an environmentally varied landscape with high anthropic impact (Chapter 4). These associations are, in turn, related to the 4.2 ka BP event, and suggest that the climatic conditions were locally humid and temperate, meaning the Sierra de Atapuerca did not experience the increases in dryness that the southern Mediterranean regions did during this period (Chapter 4). The pellets were formed within a short frame time, over the course of hours or days depending on predation and digestion, and were preserved as a result of the special conditions of the cave, in a human burial context. Therefore, the assemblages of amphibians and reptiles from the pellets allow us to reconstruct contemporaneous herpetofauna associations unlike the normal accumulations from archaeological levels, which tend to be made up of remains from a variety of sources and, possibly, different times.

The associations of amphibians and reptiles from MIR4 and MIR5 are an interesting case study, as they represent a concurrence of thermophilic, generalist and Eurosiberian species that only currently occurs in three 10x10 km UTM squares on the Iberian Peninsula. In this chapter, we look at the peculiarities of these associations in the paleobiogeographic context of the herpetofauna during the Late Quaternary and the development of modern herpetofauna assemblages from the northern Iberian Peninsula. The location of the Sierra de Atapuerca, at a crossroads between the basins of the rivers Ebro and Duero and also situated between the Cantabrian Mountains and the Sierra de la Demanda of the Iberian Mountain System, makes it a key point for understanding the

changes in the distribution of species in the northern Iberian Peninsula.

For this purpose, we performed a statistical analysis of the herpetological occurrences of the last 60,000 years from northern archaeo-paleontological sites, including the associations from MIR5 and MIR4. We aimed to put these associations in the context of the expansion of Mediterranean/thermophile species to the northern Iberian Peninsula from the southern regions, as well as to discuss the survival of species from colder climates and environments in areas that are currently Mediterranean.

5.2. El Mirador cave

El Mirador cave (*Cueva de El Mirador*) is located on the slopes of the southern tip of the Sierra de Atapuerca, within the municipality of Ibeas de Juarros, as part of the Atapuerca karst system. It is located at 42º 20' 58" N and 03º 30' 33" W and it rises to 1,033 m.a.s.l. (Figure 3.1) over the middle basin of the Arlanzón River. The cave is currently 23 metres wide by 4 metres high and 15 metres deep, and is configured as an open shelter due to the collapse of the vault (Vergès et al., 2002).

Between 1999 and 2008, the archaeological work focused on a 6 m² test pit located in the central area of the western half of the cave, where a large Holocene succession was found made up of 24 differentiated archaeological levels (Figure 3.1): Levels MIR1 and MIR2 are mixed layers formed by animal burrows and modern anthropogenic actions; MIR3 is partially disturbed, with mixed remains from the Middle to Late Bronze Age; MIR4 is a substantial level from the Middle Bronze Age, which includes at its base a secondary burial of cannibalised human bones from the Early Bronze Age that were buried during the Middle Bronze Age (Cáceres et al., 2007; Vergès et al., 2016); MIR5 is a thin level with scarce anthropogenic contributions, but it is rich in small vertebrate remains (Vergès et al., 2002). The remaining Holocene levels (MIR6–MIR24) are assigned to the Neolithic and are mostly made up of livestock pen waste, mainly *fumiers*, with the Late Neolithic represented at the top of the sequence (including MIR6) (Angelucci et al., 2009; Vergès et al., 2016).

The dating obtained on rodent bones from pellet MIR5-P21-n4 (Beta-521985: 4,530–4,417 cal BP) indicates that MIR5 is contemporaneous with the Chalcolithic collective burial in MIR203 (4,880–4,480 cal BP and 4,550–4,390 cal BP) in the northern section of the cave (sector 200) (Ceperuelo et al., 2014, 2015; Lozano et al., 2015; Vergès et al., 2016). The sedimentation in MIR5 is attributed to exclusively natural processes that occurred at a very slow speed, around 0.1 mm/year, in contrast to the 4–5 mm/year seen in the levels MIR11–16 caused by the anthropic activity of the *fumiers* (Vergès et al., 2008). This low sedimentation rate has been associated with the interruption of anthropogenic contributions during MIR5 (Vergès et al., 2002), proof of the scarcity or absence of human activities in the cave during the deposition of the sediments, since the pellets would have been rapidly disintegrated by trampling or other actions associated with human occupation. In western sector 100, another individual burial of a young man from the Middle Bronze Age (MIR106) was found on a ledge of the karst wall, dated 3,670–3,470 cal BP (Vergès et al., 2016). This burial is contemporaneous

with the base of MIR4 (3,730–3,530 cal BP) (Vergès et al., 2002, 2016).

5.3. Material and Methods

5.3.1. *Data matrix*

For the statistical analyses, the herpetofauna taxa identified in 88 levels of 19 paleo-archaeological sites chronologically dated to between early MIS 3 (ca. 60,000 BP) and the Bronze Age (ca. 3,500 BP) from the northern Iberian Peninsula (including the Ebro river and Duero river basins) were compiled into the data matrix (Figure 5.1, Table 5.1 and Appendix 5). This studied region is currently characterised by a humid Eurosiberian climate due to the Atlantic influence, with rather cold winters and temperate summers, while the Duero Valley and the Ebro Valley areas have a very continentalised Mediterranean influence. Overall, there is a good distribution of levels throughout the studied period and all the archaeological cultures known for this region are represented: the Mousterian associated with *Homo neanderthalensis* and the Aurignacian, Gravettian, Solutrean, Magdalenian, Azilian, Microlaminar Epipaleolithic, Mesolithic, Neolithic, Chalcolithic, Bell Beaker and Bronze Age that are linked to anatomically modern humans (Table 5.1).

All the species present in each level were included. Species with a regional fossil record were grouped into the rows, while the archaeo-paleontological levels, with their corresponding taxonomic lists, were listed in the columns. Therefore, in the binary database the presence of a taxon is marked by "1" and its absence by "0" (Appendix 5).

In addition, we applied corrections to the data matrix to reduce dispersion and facilitate interpretation. The genus-level citations of the genera *Hyla*, *Lacerta* and *Vipera* from levels in the northern area have been included because of their biogeographical significance. For the same reason, the genus-level citations of *Alytes* have also been included, despite the lack of species-level identification in some cases (e.g., Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013). Due to the problems in the paleontological literature of differentiating *R. temporaria* from *Rana iberica* by means of osteological criteria (e.g., Zubeldia et al., 2007; Murelaga et al., 2011; García-Ibaibarriaga et al., 2015), these two species were grouped together as *R. temporaria-iberica* in the data matrix of the northern region.

The citations of *Elaphe* sp., a snake genus that was previously grouped together with the current species *Zamenis scalaris* and *Zamenis longissimus*, were assigned to *Z. scalaris* in the case from Las Orcillas-1 (Navarre), in accordance with the Iberian thermophilic tendencies of the herpetofauna association from this site (Fernández et al., 2010). However, we did not include the citations at the genus level for genera that have two or more species represented today on the Iberian Peninsula (e.g., genera *Bufo* sensu lato and *Natrix*). The citations of *Tarentola mauritanica* and *Calotriton asper* from Cova Colomera (López-García et al., 2010a) were excluded from the data matrix to avoid statistical deviations, although they are included in the subsequent discussion.

Sites	Code	Levels	References
1. Askondo	ASK	13, 9, 8, 7, 6, 5, 3, 2 and 1	Garete and Rios-Garaizar, 2011; García-Ibaibarriaga et al., 2015
2. Cueva del Conde	CND	N104, N103, N10b, N20a, N2a1 and N2a2	Arbizu et al., 2005; López-García et al., 2011c
3. Cobrante	COB	N7 to N1	Rasines, 2009; Martín et al., 2009
4. El Portalón	POR	P16 to P1	Carretero et al., 2008; Ruiz-Zapata et al., 2008; López-García et al., 2010b
5. Cova Eirós	EIR	3 and 2	Rey-Rodríguez et al., 2016
6. Antoliñako Koba	ANT	D, C, B and A	Zubeldia et al., 2007
7. Santimamiñe	SAN	Arg-o, Camr, Csn, Balm, Almp, Slnc, Arcp, Slm and Lsm	Murelaga et al., 2011; Rofes et al., 2014
8. Erralla	ERR	VI, V, IV, III and II	Esteban and Sanchiz 1985; Peman 1985; Altuna 1985
9. Valdavara-1	VAL	Lower and Upper Units	Vaquero et al., 2009; Blain et al., 2009b; López-García et al., 2011b
10. Santa Catalina	SCT	III, II and I	Arribas and Berganza, 2010; Bailon and García-Ibaibarriaga, 2014
11. Laminak II	LAM	II-I	Arribas and Berganza, 1989; Sanchiz and Esteban 1994; Peman, 1994; Berganza and Arribas, 1994
12. Aizkoltzo	AIZ	L.15-12	Murelaga et al., 2008
13. El Mirón	MRN	10 to 3	Straus et al., 2001; Sanchiz et al., 2012
14. Las Orcillas-1	ORC	C.II-I	Fernández et al., 2010
15. Peña Larga	PLR	IV-I	Castaños 1997; Murelaga et al., 2009; Rofes et al., 2013
16. Errekatxuetako Atxa	ETX	Bell Beaker level	Murelaga et al., 2007
17. Cova Colomera	COL	C15, C14-15, C12 and EE1	Oms et al., 2009; López-García et al., 2010a
18. Balsa la Tamariz	BLT	Burial sites and prehistoric settlement	Royo and Rey, 1993; Rey and Royo, 1993; Laplana and Cuenca-Bescós, 1995
19. Peña de Estebanvela	PEV	VI, IV, III, II and I	Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013; Cacho et al., 2013

Table 5.1.- List of the latest Pleistocene-Late Holocene archaeo-palaeontological sites and levels included in the data matrix from the northern Iberian Peninsula. The codes for the Correspondence Analyses are provided. For geographical location, see Figure 5.1. in the next page.

In order to compare the fossil record with the current herpetofauna concurrence in the Sierra de Atapuerca, we collected data on the present-day herpetofauna assemblage from the same 10x10 km UTMs as the archaeo-paleontological sites included in the regional data matrices, using the "Species per UTM" function on the Spanish Server for Information on Amphibians and Reptiles (SIARE for its initials in Spanish, *Sistema de Información de Anfibios y Reptiles de España*) application website (AHE, 2020). This database also includes the new citations provided by the author for current Atapuerca herpetofauna, collected between 2016 and 2019, which can be consulted in the appendices (Appendix 6).

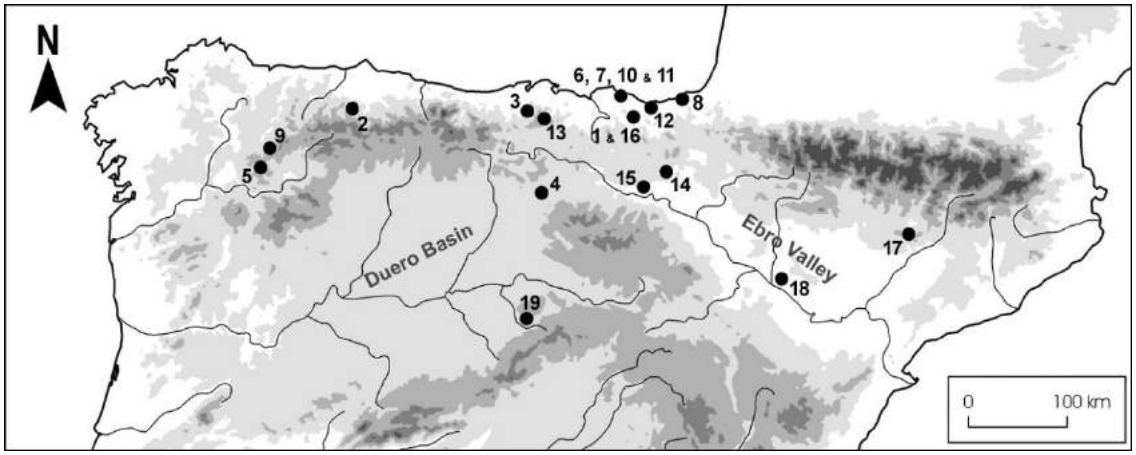

Figure 5.1.- Map with the latest Pleistocene-Late Holocene archaeo-palaeontological sites with herpetological assemblages from northern Iberian regions: **1)** Askondo, **2)** Cueva del Conde, **3)** Cueva de Cobrante, **4)** El Portalón, **5)** Cova Eirós, **6)** Antoliñako Koba, **7)** Santimamiñe, **8)** Erralla, **9)** Valdavara-1, **10)** Santa Catalina, **11)** Laminak II, **12)** Aizkoltzo, **13)** El Mirón, **14)** Las Orcillas-1, **15)** Peña Larga, **16)** Dolmen of Errekatxuetako Atxa, **17)** Cova Colomera, **18)** Balsa la Tamariz, and **19)** Peña de Estebanvela.

5.3.2. *Statistical methodology*

A correspondence analysis was used on the data matrix. This is the recommended method for comparing assemblages (assigned to the column) with the taxa they include (assigned to the rows) in an equivalent way (Greenacre, 2010). Here, its aim was to mark the relationships of proximity between the taxa of different associations, grouping them more closely than the more atypical taxa, which appear in an eccentric position in relation to the rest of the set. The Paleontological Statistics program (PAST3) was used for all statistical approaches (Hammer et al., 2001).

5.4. Results

For the prehistoric sequence of the northern region, the most prevalent species are *Rana temporaria* (or *R. temporaria-iberica*) (present in 75 assemblages, 85.2% of the total), *Anguis fragilis* (38 assemblages, 43.2%), *Epidalea calamita* (36 assemblages, 40.9%) and, to a lesser extent, *Bufo* gr. *B. bufo* (34 assemblages, 38.6%), the genus *Alytes* (32 assemblages, 36.4%) and the genus *Vipera* sp. (20 assemblages, 22.7%) (Appendix 5). The rest of the taxa are present in a lower number of concurrences (between 1 and 8). The least representative taxa are *Zamenis scalaris* and *Hierophis viridiflavus* (2 assemblages, 2.2%), and *Chioglossa lusitanica*, *Discoglossus galganoi* and *Vipera latastei* (1 assemblage, 1.1%).

The correspondence analysis performed on the herpetofauna taxa from northern Iberia demarcated three separate groups (Figure 5.2). The first group is made up of the species *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria-iberica*, *A. fragilis* and the genera *Alytes* and *Vipera aspis/seoanei*. These taxa are Eurosiberian or generalist taxa that tolerate cold weather conditions.

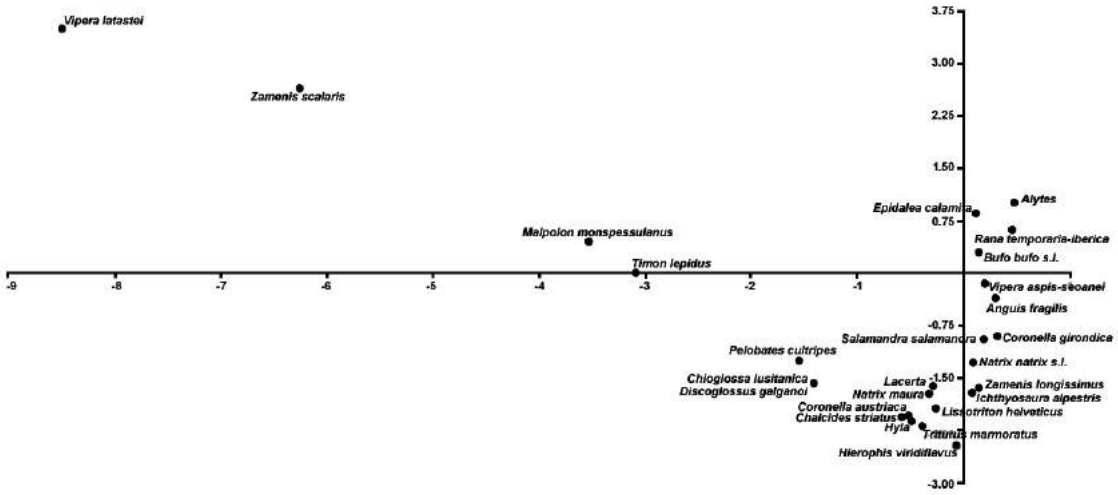

Figure 5.2.- Correspondence Analysis of the taxa from the northern region of the Iberian Peninsula between the latest Pleistocene to Late Holocene.

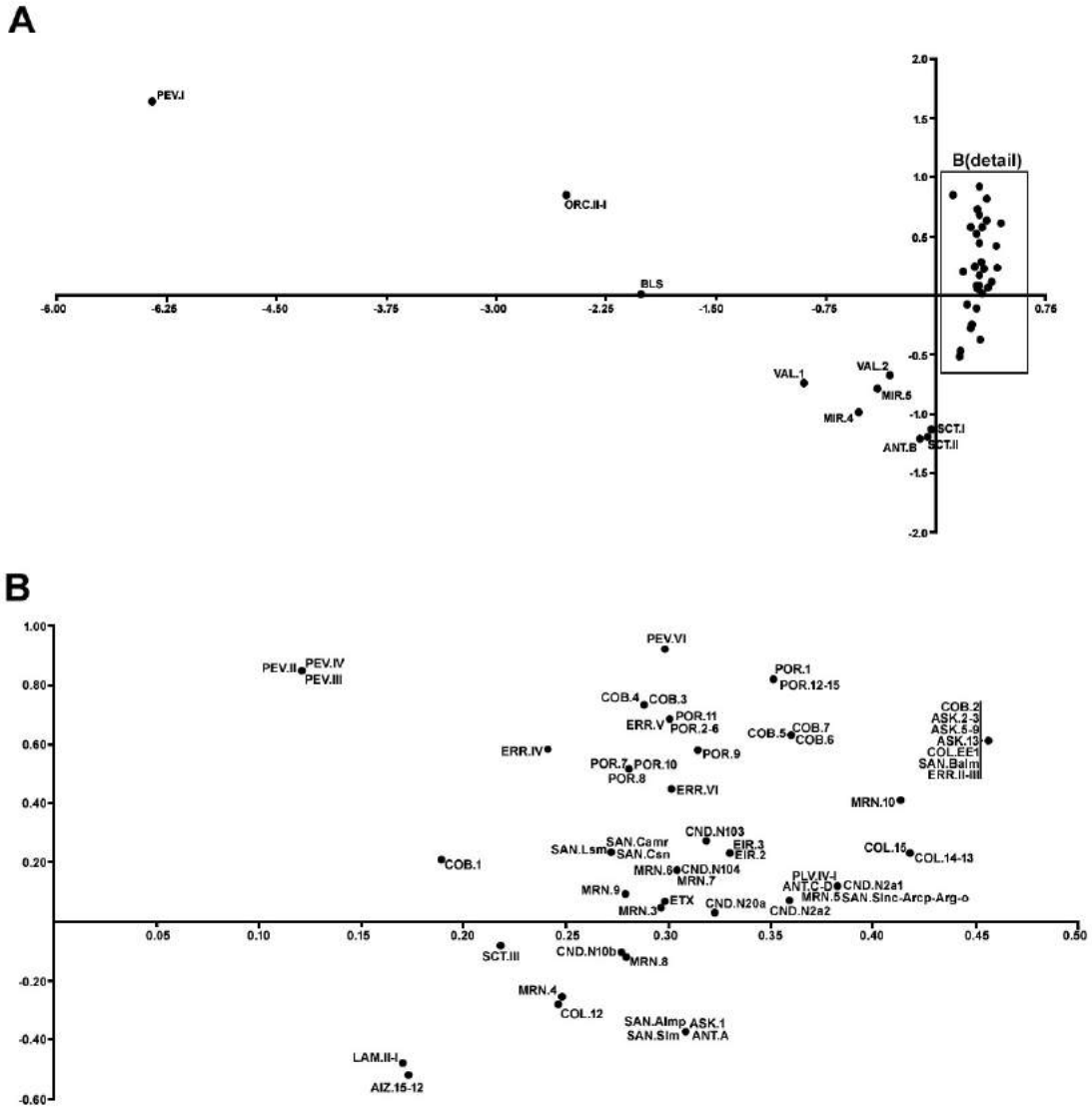

Figure 5.3.- Correspondence Analysis of the herpetofaunal assemblages from the northern region of the Iberian Peninsula between the latest Pleistocene to Late Holocene.

The second group comprises the species *Ichthyosaura alpestris*, *Lissotriton helveticus*, *Salamandra salamandra*, *Chalcides striatus*, *Hierophis viridiflavus*, *Coronella austriaca*, *Coronella girondica*, *Natrix maura*, *Natrix natrix*, *Zamenis longissimus*, and the genera *Hyla* and *Lacerta*. All are hygrophilous and/or generalist taxa, tolerant of Eurosiberian and/or mild-Mediterranean influences.

Finally, the third group in the regional cluster is made up of *Chioglossa lusitanica*, *Discoglossus galganoi*, *Pelobates cultripes*, *Timon lepidus*, *Zamenis scalaris*, *Malpolon monspessulanus* and *Vipera latastei*. Except for *C. lusitanica*, which is a salamander endemic to the north-western Iberian sector (Vences, 2002), the remaining taxa are thermophilic species linked to the Mediterranean influence.

The correspondence analysis of the assemblages by levels shows a similar pattern (Figure 5.3). Level I of Peña de Estebanvela, level II-I of Las Orcillas-1, and the herpetological ensemble of Balsa La Tamariz are distributed in the upper left square. Following the same axis of dispersion are the herpetological associations from levels 1 and 2 of Valdavara-1, level B from Antoliñako Koba, levels II and I from Santa Catalina, as well as the associations of reptiles and amphibians from the pellets of MIR4 and MIR5 (Figure 5.3.A).

The remaining associations of the regional record appear highly concentrated on the right side of the graph, following the vertical axis (Figure 5.3.B).

5.5. Discussion

5.5.1. *MIR4 and MIR5 in the north-Iberian herpetofaunal context*

The proximity relationships marked by the correspondence analyses were interpreted according to biogeographical criteria: they brought together the concurrences from MIR4 and MIR5 with the Holocene associations of Santa Catalina (levels II and I) and Valdavara-1 (Upper and Lower Units). MIR4 and MIR5 are positioned in the middle between the associations of the Ebro Valley (Balsa la Tamariz and levels II-I of Las Orcillas-1) and the south of the Duero basin (level I of Peña de Estebanvela), which are mainly thermophilic, and the rest of the associations from the northern Iberian Peninsula, which have been comprised of mostly the same Eurosiberian and generalist species since MIS 3.

The scenario proposed by the statistical results are concordant with the analyses presented Chapter 1. The dominant association for the northern Iberian Peninsula consists of *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria-iberica*, *A. fragilis* and the genera *Alytes* and *Vipera sp.* (plausibly *Vipera aspis/seoanei*). These taxa are typical in the fossil record from northern Iberian regions during MIS 2, the last glacial phase, and they comprised, almost exclusively, all the associations during MIS 3. The second group is made up of the species *I. alpestris*, *L. helveticus*, *S. salamandra*, *C. striatus*, *H. viridiflavus*, *C. austriaca*, *C. girondica*, N. *maura*, *N. natrix*, *Z. longissimus*, and genera *Hyla* and *Lacerta* (*Lacerta bilineata* and possibly *Lacerta schreiberi*). With the exception of *S. salamandra*, recorded in the Cueva del Conde and attributed to MIS 3 (López-

García et al., 2011c), all are hygrophilous and/or generalist taxa tolerant of a Eurosiberian influence that appear in the regional fossil record during MIS 1, after the Last Glacial Maximum. Finally, the third group is made up of *C. lusitanica*, *D. galganoi*, *P. cultripes*, *T. lepidus*, *Z. scalaris*, *M. monspessulanus* and *V. latastei*, which are mostly thermophilic species of Mediterranean influence. These seven species also appear in the north-Iberian fossil record during MIS 1. The presence of the hygrophilous *C. lusitanica* in this group is due to its unique fossil record in the herpetofauna assemblage of the Upper Unit of Valdavara-1, where other thermophilic species such as *Discoglossus* cf. *galganoi*, *T. lepidus* and *M. monspessulanus* are also represented (Blain et al., 2009b; López-García et al., 2011b).

The herpetofauna record from the northern Iberian Peninsula between the Late Mousterian and the Bronze Age (ca. 60,000 to 3,000 BP) points to the very pronounced predominance of tolerant generalist and Eurosiberian species, mainly amphibians (Chapter 1). In the herpetological concurrences of MIS 3 (ca. 60,000 to 26,900 BP) and MIS 2 (ca. 26,900 to 14,900 BP), the herpetofauna present in northern Iberian assemblages is limited to *S. salamandra*, *Alytes* sp., *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria-iberica*, *A. fragilis* and *Vipera* sp., as well as indeterminate Salamandridae, Lacertidae and Colubrinae, and the possible presence of *Rana dalmatina* (Esteban and Sanchiz, 1985; Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b, 2011b; Murelaga et al., 2011; Garcia-Ibaibarriaga et al., 2015). The number of species decreased during MIS 2 and the Last Glacial Maximum and the composition was mainly reduced to *Alytes* sp., *E. calamita*, *Bufo* gr. *B. bufo*, *R. temporaria-iberica*, possibly *R. dalmatina*, *A. fragilis*, Lacertidae indet., and *Vipera* sp. (Esteban and Sanchiz, 1985; Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b; Murelaga et al., 2011).

During MIS 1 (ca. 14,900 BP to present) and especially since the Holocene (ca. 11,700 BP to present), the taxa *I. alpestris*, *C. striatus*, *C. lusitanica*, *C. austriaca*, *C. girondica*, *D. galganoi*, *H. viridiflavus*, *Hyla* sp. (*Hyla molleri*?), *Lacerta* s.l., *L. helveticus*, *M. monspessulanus*, *N. maura*, *Natrix natrix* s.l. (*Natrix astreptophora?*), *T. lepidus*, *T. marmoratus*, *Zamenis l.* and *Z. scalaris* appear in the herpetological record of the region, linked to post-glacial climate warming, although they remain in the minority (Chapter 1). The dominant taxa during MIS 3 and MIS 2 in the northern Iberian Peninsula continued to be those most documented during MIS 1. The concurrences from levels IV, III and II of Erralla (Esteban and Sanchiz, 1985), from the levels Balm, Almp, Slnc, Arcp, Slm and Lsm of Santimamiñe (Murelaga et al., 2011), from level 2 of Cobrante (Martín et al., 2009), levels 3 and 2 of Askondo (Garcia-Ibaibarriaga et al., 2015), level A of Antoliñako Koba (Garcia-Ibaibarriaga et al., 2015) and the Bell Beaker level from the dolmen of Errekatxuetako Atxa (Murelaga et al., 2007) are made up exclusively of one or more of these taxa: *Alytes* sp., *E. calamita*, *Bufo* gr. *B. bufo*, *A. fragilis*, *Vipera* sp. and, particularly, *R. temporaria* (or *Rana temporaria-iberica*).

The arrival of thermophilic species is detected for the first time in the Lower Unit of Valdavara-1 (Galicia) via the presence of *M. monspessulanus*, which is linked to a warm climate phase

during the Bölling-Allerød interstadial (15,120±70 BP–13,770±70 BP; Vaquero et al., 2009; López-García et al., 2011b). This snake appears together with other typically hygrophilous species, such *Lacerta* s.l. (plausibly *Lacerta* sensu stricto), *Coronella* cf. *austriaca*, *N. maura* and *N. natrix* s.l., as well as *S. salamandra*, which reappears for the first time in the northern fossil record since its last presence in level N2a2 of Cueva del Conde in MIS 3 (López-García et al., 2011c). The Upper Unit of Valdavara-1 (4,490±40 BP; Vaquero et al., 2009) presents a more recent assemblage with the presence of thermophilic Mediterranean and hydro-hygrophilous species. This assemblage is made up of *C. lusitanica*, *Discoglossus* cf. *galganoi*, *Bufo* gr. *B. bufo*, *R. iberica*, *C. striatus*, *A. fragilis*, *T. lepidus*, *N. maura*, *Coronella* cf. *austriaca*, *M. monspessulanus* and *Vipera* sp. (Blain et al., 2009b; López-García et al., 2011b). The Upper Unit of Valdavara-1 corresponds to the first citations in the north-western Iberian area for *C. lusitanica*, *D. galganoi*, *C. striatus* and *T. lepidus*.

For the Cantabrian coastal area, there are three diverse herpetofauna associations of a marked hydro-hygrophilous character from levels III, II and I of Cueva de Santa Catalina (Basque Country) that cover the terminal Pleistocene to early Holocene (N.III: 12,425±90 BP and 12,345±85 BP; N.II: 11,155±80 BP; N.I: 10,530±110 BP and 9,180±110 BP; Arribas and Berganza, 2010). These associations include the first regional records for *I. alpestris*, *L. helveticus* (cf. *Lissotriton helveticus*), *T. marmoratus* (*Triturus* cf. *marmoratus*), *Hyla* sp., *C. striatus*, *C. girondica* (*Coronella* cf. *girondica*), *H. viridiflavus* (cf. *Hierophis viridiflavus*) and *Z. longissimus* (cf. *Zamenis longissimus*) (Bailon and García-Ibaibarriaga, 2014), a mixture of Eurosiberian hydro-hygrophilous species typically from and/or tolerant of the Atlantic climate, and two Mediterranean-tolerant snake species (*H. viridiflavus* and *Z. longissimus*) of trans-Pyrenean origins with no previous fossil record on the Iberian Peninsula (Nagy et al., 2002; Joger et al., 2007; Musilová et al., 2010).

The association of *E. calamita*, *T. lepidus*, *M. monspessulanus*, *Z. scalaris*, cf. *Coronella* sp. and *V. latastei* is recorded from level I of Estebanvela de Peña (11,330±50 BP–10,640±60 BP; Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013). This assemblage is made up of markedly thermophilic herpetofauna and is assigned to the cold climatic phase, which indicates a climate scenario that was less aggressive in the Iberian inland for the thermophilic and Mediterranean species during the latest Pleistocene and earliest Holocene. It also shows that thermophilic Mediterranean species were inhabiting the southern region of the Duero Basin and the northern slope of the Central Mountain System at the beginning of the Holocene, from where they could have colonised the northernmost territories through the Northern Castilian Plateau.

In the northern Ebro Valley, the herpetofauna assemblage from levels C.II–I of Las Orcillas-1 (Navarre) (8,610±50 BP, Fernández et al., 2010) consists of *Bufo* gr. *B. bufo*, *E. calamita*, *T. lepidus*, *M. monspessulanus*, *Natrix* sp. and *Zamenis-Rhinechis* (= *Elaphe* sp. sensu lato) (Fernández et al., 2010). This assemblage includes two thermophilic Mediterranean species, the lizard *T. lepidus* and the snake *M.*

monspessulanus, making it the oldest Holocene record for *T. lepidus* in the northern Iberian Peninsula. It also includes the possible presence of *Z. scalaris*, another Mediterranean species typical of dry environments and warm climates. The association of *E. calamita*, *P. cultripes*, *T. lepidus* and *M. monspessulanus* from Balsa la Tamariz, a Bronze Age settlement in the middle Ebro Valley (ca. 3,600–3,400 BP; Laplana and Cuenca-Bescós, 1995), also has markedly Mediterranean and thermophilic affinities. The fully thermophilic Mediterranean gecko *T. mauritanica* is only recorded in level A.sup of Cova Colomera (3,490±50 BP; López-García et al., 2010a), and was not included in the data matrix to avoid statistical deviations. This last archaeological site is located on one of the tributary valleys of the Ebro river.

The prehistoric assemblages from Orcillas-1, Balsa la Tamariz, Cova Colomera and Valdavara-1 possibly indicate the existence of two expansion routes towards the north of the Iberian Peninsula for species of Mediterranean influence and for hygrophilous species less tolerant of cold climates and glacial conditions. The eastern route, represented by Orcillas-1, Balsa la Tamariz and Cova Colomera would consist of the Ebro Valley and, according to the fossil record, would have been used by Mediterranean herpetofauna (*P. cultripes*, *T. mauritanica*, *T. lepidus*, *M. monspessulanus*, and possibly *Z. scalaris*). The western route, marked by Valdavara-1, would be located on the Atlantic coastline running towards the Galician coasts and would have been used by species of Mediterranean origin (*D. galganoi*, *T. lepidus* and *M. monspessulanus*) as well as typically western species (*C. lusitanica* and *L. schreiberi*) and generalist and/or tolerant species (*N. maura* and *C. striatus*) to colonise north-western Iberia and the Cantabrian fringe. Probably, the herpetofauna of level I of Peña de Estebanvela would represent a third route, from the northern Central Mountain System through the Duero Basin. At the same time, the hydro-hygrophilous population of Santa Catalina could be related to a refuge located on the Cantabrian coast but also another refuge in the south of France, from where some species (e.g., *L. bilineata*, *H. viridiflavus*, *Z. longissimus*) would have crossed the Pyrenees.

In conclusion, the main biogeographical movements observed in the northern Iberian Holocene converge in the herpetofauna assemblages of the El Mirador pellets. The associations of amphibians and reptiles from MIR4 and MIR5 have taxa compositions that largely correspond to the taxa surviving in the northern Iberian Peninsula during MIS 3 and MIS 2 and link them biogeographically to the Eurosiberian region. But, in turn, these same associations concurrently contain the fully thermophilic and Mediterranean species *P. cultripes* and *T. lepidus*, indicating the existence of a Mediterranean influence in the area, which is analogous to that present at other sites from the same region. Hydro-hygrophilous taxa that appear in the northern fossil record during MIS 1, such as *L. helveticus*, *T. marmoratus*, *Hyla* gr. *H. arborea* (*H. molleri*) and *Lacerta* cf. *bilineata*, were also documented in the pellets. The location of Sierra de Atapuerca in a natural corridor between the Ebro Valley and the Duero River Basin may explain this mixture of

biogeographical influences, as a crossroads of post-glacial colonisation routes for the southern Iberian herpetofauna. Its proximity to the Cantabrian area of Atlantic influence would also allow the arrival of hydrophilic species, probably from the north-west or north.

5.5.2. *Changes in the composition of amphibian and reptile species in the Sierra de Atapuerca during the last 30,000 years*

The existence of a large number of archaeo-paleontological sites in the Sierra de Atapuerca from the Lower Pleistocene to the Late Holocene has allowed us to examine the presence of herpetofauna over an extended period of time at a local level. Specifically, the sequence of El Portalón cave covers part of the period under study.

This is an archaeo-paleontological site located at the current entrance to Cueva Mayor, a cave belonging to the karst system of the Sierra de Atapuerca. Two large stratigraphic units have been identified at this site, the upper one comprised of nine levels that span from the Neolithic to the Iron Age, and the lower sequence from the Late Pleistocene, corresponding to level 10 and consisting of sixteen sub-levels (Carretero et al., 2008; Ruiz-Zapata et al., 2008). Two sub-levels have been dated: sub-level P1 (16,890±80 BP) and sublevel P11 (30,300±190 BP) (Carretero et al., 2008; Ruiz-Zapata et al., 2008; López-García et al., 2010b). Herpetofauna associations have been found at all sub-levels and they include the typical MIS 3 and MIS 2 species of the northern Iberian Peninsula, without exception (López-García et al., 2010b).

The herpetofauna associations with the largest number of taxa occur at sub-levels 10, 8, and 7 and especially at sub-level 4 of El Portalón, which is ascribed to the Last Glacial Maximum, and are made up of *A. obstetricans*, *Bufo* gr. *B. bufo*, *E. calamita*, *R. temporaria*, Lacertidae indet. and *Vipera* sp. A single specimen of Colubrinae indet. was recovered in sub-level 14 (López-García et al., 2010b). These taxa are also represented in the pellets of MIR4 and MIR5, where, in addition, we found *L. helveticus*, *T. marmoratus*, *P. cultripes*, *H.* gr. *H. arborea* (*H. molleri*), *A. fragilis*, *C. striatus*, *Lacerta* cf. *bilineata*, *T. lepidus* and *Coronella* cf. *austriaca*. This association is partially represented in the current Atapuerca herpetofauna (Table 5.2).

Of the herpetofauna from the pellets, *P. cultripes*, *R. temporaria*, *C. austriaca* and *V. aspis/seoanei* have currently disappeared from Sierra de Atapuerca and its surroundings. Instead, *S. salamandra*, *D. galganoi*, *Pelodytes punctatus*, *Pelophylax perezi*, *Blanus cinereus*, *C. girondica*, *N. astreptophora*, *N. maura*, *Z. scalaris* and *V. latastei* now inhabit this area. Most of these species are thermophilic and Mediterranean, in accordance with the current continentalised Mediterranean climate.

The apparent absence of *P. cultripes* is probably due to the lack of surveys, because this species can be found in areas in close proximity to the site. For example, in 2019 a western spadefoot toad was identified 30 km north of Atapuerca (author's observation in square VN42; Appendix 6).

Species	Late Pleistocene MIS3 and MIS2 El Portalón 14-1 sub-levels	Mid-Late Holocene MIS1 MIR4 and MIR5 pellets	Today MIS1 10x10 km UTM VM58 and VM59
Lissotriton helveticus		■	■
Triturus marmoratus		■	■
Salamandra salamandra			■
Alytes obstetricans	■	■	■
Discoglossus galganoi			■
Pelodytes punctatus			■
Pelobates cultripes		■	
Hyla molleri / *Hyla* gr. *H. arborea*		■	■
Bufo spinosus / *Bufo* gr. *B. bufo*	■	■	■
Epidalea calamita		■	■
Pelophylax perezi			■
Rana temporaria	■	■	
Blanus cinereus			■
Anguis fragilis		■	■
Chalcides striatus		■	■
Lacerta bilineata		■	■
Podarcis liolepis			■
Timon lepidus		■	■
Lacertidae indet.	■	■	■
Coronella austriaca		■	
Coronella girondica			■
Natrix astreptophora			■
Natrix maura			■
Zamenis scalaris			■
Colubrinae indet,	■		
Vipera aspis/seoanei		■	
Vipera latastei			■
Vipera sp.	■		

Table 5.2.- Synthesis of the herpetofauna from Sierra de Atapuerca during the Late Quaternary.

Another possibility is that the western spadefoot toad is actually extinct at the local level, due to changes in agriculture such as new ploughing methods which reach greater depths and may negatively affect the populations of *P. cultripes* in their underground burrows.

For the snake *C. austriaca*, current populations have been documented in nearby squares, both to the north and to the east, in the Sierra de la Demanda and northern Páramos (Diego-Rasilla and Ortiz-Santaliestra, 2009, AHE, 2020; own data, Appendix 6). Both *V. seoanei* and *V. aspis* have populations a few dozen kilometres to the north, and the retraction of their territory is possibly related to competition from *V. latastei*, which is currently very abundant in the Sierra de Atapuerca (own data, Appendix 6). The north-central zone of Burgos is the only site on the Iberian Peninsula

where these three species of viper can be found together, and are even hybridising (Martínez-Freiría et al., 2006, 2008, 2009, 2010; Tarroso et al., 2014). In the case of *R. temporaria*, the contraction of its distribution range is more evident. This brown frog is currently absent from the Sierra de Atapuerca and its closest populations are located 60 kilometres to the north and northeast, already within the Eurosiberian bio-region (Diego-Rasilla and Ortiz-Santaliestra, 2009, AHE, 2020; own data, Appendix 6).

To conclude, the herpetofauna record of the last 30,000 years in the Sierra de Atapuerca depicts an evident change towards a greater Mediterranean warm component during the Holocene, to the detriment of the Eurosiberian cold component. The first phase is represented by the herpetofauna assemblages from El Portalón, which are made up of Eurosiberian and tolerant generalist species that lived during MIS 3 and MIS 2. The associations of reptiles and amphibians from the pellets of MIR4 and MIR5 show an intermediate second phase, with a concurrence formed mainly by hydro-hygrophilous species with Eurosiberian affinities but in which Mediterranean thermophilic species already appear. The current herpetofauna of Atapuerca presents the third phase with a mostly Mediterranean composition, in which the hydro-hygrophilous species or those with Eurosiberian affinities have been confined to areas where a high degree of humidity is maintained, such as the riparian forests of the Arlanzón River and its tributaries or some areas with water sources emanating from the Sierra de Atapuerca itself (Appendix 6).

5.6. Conclusions

The contextualisation of the fossil herpetofauna associations from MIR4 and MIR5 within the north-Iberian Latest Quaternary record has made it possible to position them within the process of post-glacial northern expansion. Their compositions are a mixture of generalist and Eurosiberian taxa, hygrophilous and Mediterranean thermophilic species. The geographical location of the Sierra de Atapuerca, in a natural corridor between the Duero River Basin and the Ebro Valley, and between the Iberian Mountain System and the Cantabrian Mountains, would have allowed species of multiple biogeographical origins to reach the area during the Holocene.

Comparing the Latest Pleistocene herpetofauna from El Portalón (Sierra de Atapuerca) with modern herpetofauna indicates a progressive evolution from a herpetofauna with Eurosiberian affinities and cold-climate contexts to the current situation, in which warmer Mediterranean thermophilic species predominate. The herpetofauna contained in the pellets of MIR4 and MIR5 may represent an intermediate phase, sharing Eurosiberian, hydro-hygrophilous and Mediterranean thermophilic herpetofauna. Future efforts in the analysis of the herpetofauna from the other levels of the El Mirador sequence will allow us to study the timeline of this process throughout the Holocene, in the context of the arrival of thermophilic Mediterranean species and the extirpation of the Eurosiberian species.

Supplementary data

Appendix 5. Supplementary Table 5.S1.- Data matrix of the northern regions with significative herpetofaunal assemblages from the latest Pleistocene to the Late Holocene, including El Mirador pellets (pages 232-234).

Appendix 6. Current herpetological records of prospecting surveys in the province of Burgos, 2016-2019 (pages 235-293).

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BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Chapter 6

Trade and stowaways: molecular evidence for human-mediated translocation of eastern skink into the western Mediterranean

Abstract

Human movements in the regions surrounding the Mediterranean Sea have caused a great impact in the composition of terrestrial fauna due to the introductions of several allochthonous species, intentionally or not. Reptiles are one of the groups where this anthropic impact is most evident, owing to the extensive intra-Mediterranean dispersals of recent chronologies. *Chalcides ocellatus* is a widespread skink with a natural distribution that covers almost the entire Mediterranean Basin. Two hypotheses have been proposed to explain its origin: natural dispersions and human translocations. Previous molecular data suggest the occurrence of a recent dispersal phenomenon across the Mediterranean Sea. In this study we present the first record of this species in the Iberian Peninsula, from Serra del Molar (South-east Spain). We combined molecular analyses and archaeological records to study the origin of this population. The molecular results indicate that the population is phylogenetically closely related to specimens from north-eastern Egypt and southern Red Sea. We suggest that the species arrived at the Iberian Peninsula most likely through human-mediated dispersal by using the trade routes. Between the Iron to Middle Ages, even now, the region surrounding Serra del Molar has been the destination of human groups and commercial goods of Egyptian origins, in which *Chalcides ocellatus* could have arrived as stowaways. The regional geomorphological evolution would have restricted its expansion out of Serra del Molar. These findings provide new data about the impact of human movements on faunal introductions and present new information relating to mechanisms of long-distance translocations.

6.1. Introduction

The Mediterranean Basin has been and still is a fascinating biogeographical framework presenting constant faunal exchanges, which have affected many of the faunas present on every shore of the Mediterranean and which have been augmented by human intervention (Pooley and Queiroz, 2018). The distribution and inferred phylogeographic patterns of reptiles such as the circum-Mediterranean geckos *Tarentola mauritanica* and *Hemidactylus turcicus* have suggested the existence of possible human interventions in their intra-Mediterranean dispersals (Harris et al., 2004; Carranza and Arnold, 2006; Rato et al., 2011, 2016; Stöck et al., 2016). This phenomenon has also affected the Iberian Peninsula, which shares many species, both reptiles and amphibians, with North Africa (Pleguezuelos et al., 2008). Human translocations with North African origin are proposed for the Iberian populations of the chameleon *Chamaeleo chamaeleon* (Paulo et al., 2002) and the treefrog *Hyla meridionalis*

(Recuero et al., 2007). Other dispersals, on the other hand, have their origins in the Iberian Peninsula, for example, the translocation of the lizard *Podarcis vaucheri* in Greece (Spilani et al., 2018). In the Western Mediterranean context, the human-mediated introductions of herpetofauna in the Balearic Islands stand out, where the successive arrivals of different human groups led to the extirpation of native species in most of the main islands (*Alytes muletensis* and *Podarcis lilfordi*), besides the introduction of new species from other Mediterranean regions (e.g., *Bufotes balearicus*, *Emys orbicularis*, *Testudo hermanni*, *Podarcis sicula*, and *Hemorrhois hippocrepis*), from the Neolithic-Bronze Ages to the present (Pinya and Carretero, 2011; Valenzuela et al., 2016; Silva-Rocha et al., 2018).

Another reptile species with a practically circum-Mediterranean distribution is the ocellated skink, *Chalcides ocellatus*, which can be considered a species complex, with several deep lineages across North Africa (Carranza et al., 2008). This skink is widely distributed in the southern, central and eastern regions of the Mediterranean basin (Figure 6.1), from the eastern Moroccan coast to Anatolia, as well as on various islands in the Aegean Sea, Euboea, Crete, Cyprus, Tunisian Tabarka, Malta, Sicily, Conigli, Lampedusa, Lampione, Linosa and Sardinia, with continental European populations in and into the Attica peninsula (Kornilios et al., 2010). The species' distribution range also extends to the Near East, Mesopotamia, and the shores of the Red Sea, as far south as Somalia and Yemen, and in the Persian Sea region as far east as Pakistan; (Anderson, 1999; Lavin and Papenfuss, 2012). There are currently introduced populations in Naples, Stromboli, Kasos and Sri Lanka (Caputo et al., 1997; Karunarathna et al., 2009; Lo Cascio and Grita, 2016; Kornilios and Thanou, 2016), as well as in Florida and Arizona (Krysko et al., 2011; Gunn et al., 2012). Three Algerian individuals were released in Marseille (France) and created a new population during the first decades of the 20th century, and an isolated individual was found in the railway goods yards of Cardiff (Walles) in 1944 (Siépi, 1913; Fitter, 1959; Kraus, 2009).

The large transcontinental distribution of *C. ocellatus*, together with the low molecular divergence and the hard polytomies observed among many of the populations assigned to the eastern subclades, have made it possible to postulate the human-mediated introduction in recent times as a possible mechanism for its expansion (Kornilios et al., 2010; Lavin and Papenfuss, 2012), and even link it, at least in the context of the Mediterranean Sea, to the trade during the Ancient Age (Kornilios et al., 2010).

In this study, we report for the first time the presence of a reproductive population of the ocellated skink, *C. ocellatus*, in Serra del Molar (Figure 6.2). The geographic location of the population is a small coastal mountainous area in the southeast of the Iberian Peninsula, localised between the Mediterranean Sea and marsh areas originated by the Vinalopó and Segura rivers, in the southern Valencian Country. These individuals were morphologically identified as *C. ocellatus* (body elongate and cylindrical, tail almost equal to body length, ear without

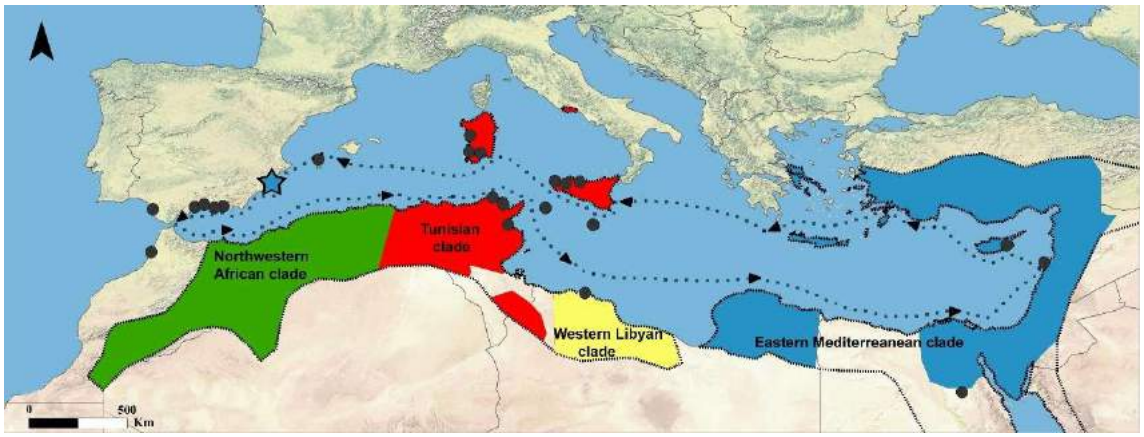

Figure 6.1.- Mediterranean distribution range of *Chalcides ocellatus* according to its phylogenetic clades (Kornilios et al., 2010) and the geographic location of the Serra del Molar population (SE Iberian Peninsula; blue star). Arrows indicate the Phoenician intra-Mediterranean maritime routes and the main trade ports during the first Iron Age period (black dots) (based on Aubet, 2009).

lobules, tympanum exposed, multiple dorsal *ocelli*; Baha El Din, 2006). Given that this is a species without current herpetological or archaeo-palaeontological records in the Iberian Peninsula, molecular analyses were performed to confirm its identification and to determine the biogeographical origin of this newly discovered population.

6.2. Material and methods

Individuals of *C. ocellatus* were identified for the first time in April 2017 in Serra del Molar (38.1439N, -0.6569W, WGS; Figure 6.1). This area is part of the Elx municipality, in the Baix Vinalopó comarca within the Valencian province of Alacant/Alicante, in the grid UTM 30SYH02. The area where the discovery took place is between 35 and 75 meters above sea level, presents a Mediterranean thermos-type and is biogeographically located in the Alicantino subsector of the Murciano-Almeriense sector (Rivas-Martínez, 1987). It is a predominantly sedimentary area, formed at its base by calcareous sandstones of coastal marine origin on which outcrop conglomerates of silt, marl and fluvio-lacustrine sands (Almela et al., 1978). The area presents the typical thermo-Mediterranean scrub communities (*Brachypodium retusum*, *Macrochloa tenacissima*, *Rosmarinus officinalis*, *Chamaerops humilis*) with concentrations of *Pinus halepensis*, and only the lower parts show evidence of abandoned plots for cultivation of olives (*Olea europaea*) and carobs (*Ceratonia siliqua*), although today most of them are covered by xerophilous and heliophilous scrubs. The archaeological remains of the Iberian settlements of La Escuera and El Oral, and the necropolis of El Molar are located in the surroundings (Grau and Moratalla, 2001). According to data from official herpetological agencies (AHE, 2018; BDB-GVA, 2018), the reptiles of this area had not been surveyed previously by any herpetologist or scientific group.

In collaboration with the Valencian environmental authorities, successive surveys were carried out in this locality to monitor their presence in the area, to obtain data on their spatial

Figure 6.2.- Individuals of *Chalcides ocellatus* from Serra del Molar (SE Iberian Peninsula): (**A**) Adult male (♂ n.3, CN12645); (**B**) Adult male (♂ n.4); (**C**) Gravid female (♀ n.2); (**D**) Adult male in its habitat (♂ n.5, CN13391).

distribution and morphology, and to obtain tissue samples for genetic analyses. Twelve identified individuals were captured to obtain morphometric data and subsequently released (Table 1). Each individual has been sexed by pressing gently around the cloacal region to find the hemipenis, if males. Importantly, this process was conducted avoiding the total eversion of hemipenis to avoid potential injuries for the animals.

6.2.1. *Genetic sampling, DNA extraction and amplification*

In order to perform molecular analyses, tissue samples were taken from five individuals with the following sample codes: CN12564 and CN12645 were collected during October 2017 (Figure 6.3), and CN13391, CN13434 and CN13435 were collected in May 2018. To understand the geographic origin of these newly discovered Valencian individuals, sequences of other *C. ocellatus* specimens from distinct localities around the Mediterranean Basin and across the species' distribution range, were retrieved from GenBank. Two specimens of *Chalcides montanus* have been included as outgroup (Carranza et al., 2008; Kornilios et al., 2010) (see Supplementary data in Appendices 7 and 8).

Genomic DNA was extracted from alcohol-preserved tissue samples using the SpeedTools Tissue DNA Extraction kit (Biotools, Madrid). A fragment of 303 bp of the mitochondrial gene Cytochrome b (*cytb*) was amplified by the Polymerase Chain Reaction (PCR).

Individuals	Body length (SVL; in *mm*)	Tail length (in *mm*)	Total length (in *mm*)	Tail/body ratio
Male n.1 (01.04.2017)	95.2	100.5	195.7	1.05
Male n.2 (01.04.2017)	85.8	91.9	177.7	1.07
Male n.3, CN12645 (07.10.2017)	99.1	101.7	200.8	1.02
Male n.4 (20.04.2018)	102.1	76.8*	178.9	0.75
Male n.5, CN13391 (18.05.2018)	97.2	73.2*	170.4	0.75
Female n.1 (02.04.2017)	96.0	92.4	188.4	0.96
Female n.2, gravid (11.06.2017)	105.1	115.4	220.5	1.09
Female n.3, gravid (11.06.2017)	89.4	90.7	180.1	1.01
Female n.4, CN12564 (08.10.2017)	84.3	86.6	170.9	1.03
Female n.5 (20.04.2018)	84.3	35.4*	119.7	0.42
Female n.6, CN13435 (18.05.2018)	78.4	89.3	167.7	1.14
Female n.7, CN13434 (18.05.2018)	76.8	83.5	160.3	1.08
Median ± Standard error (SE)	91.14 ± 2.738	86.45 ± 5.658	177.59 ± 7.115	0.95 ± 0.142
Median ± Standard error (SE) (without autotomized tails)	90.01 ± 3.265	94.67 ± 3.259	184.68 ± 6.252	1.05 ± 0.111

Table 6.1.- Morphometric data of the *Chalcides ocellatus* individuals from Serra del Molar. Specimens used for the genetic identification are with their corresponding code. (*) = autotomized and partially regenerated tails.

The following primers for amplification and sequencing were modified from Kocher et al. (1989): Cytb1 (5'-CCATCCAACATCTCAGCATGATGAAA-3') and Cytb2 (5'-CCCTCAGAATGATATTTGTCCTCA-3'). We performed PCR in a volume of 25 µl with an initial denaturation step of 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 80s, annealing at 50°C for 45s, and extension at 72°C for 1 min; final extension step was set for 72°C for 5 min. Amplicons were visualized on a 1% agarose gel stained with SYBR Safe DNA gel stain (Invitrogen Corp., Carlsbad, CA, USA). Purification and bi-directional sequencing were carried out by Macrogen (Macrogen

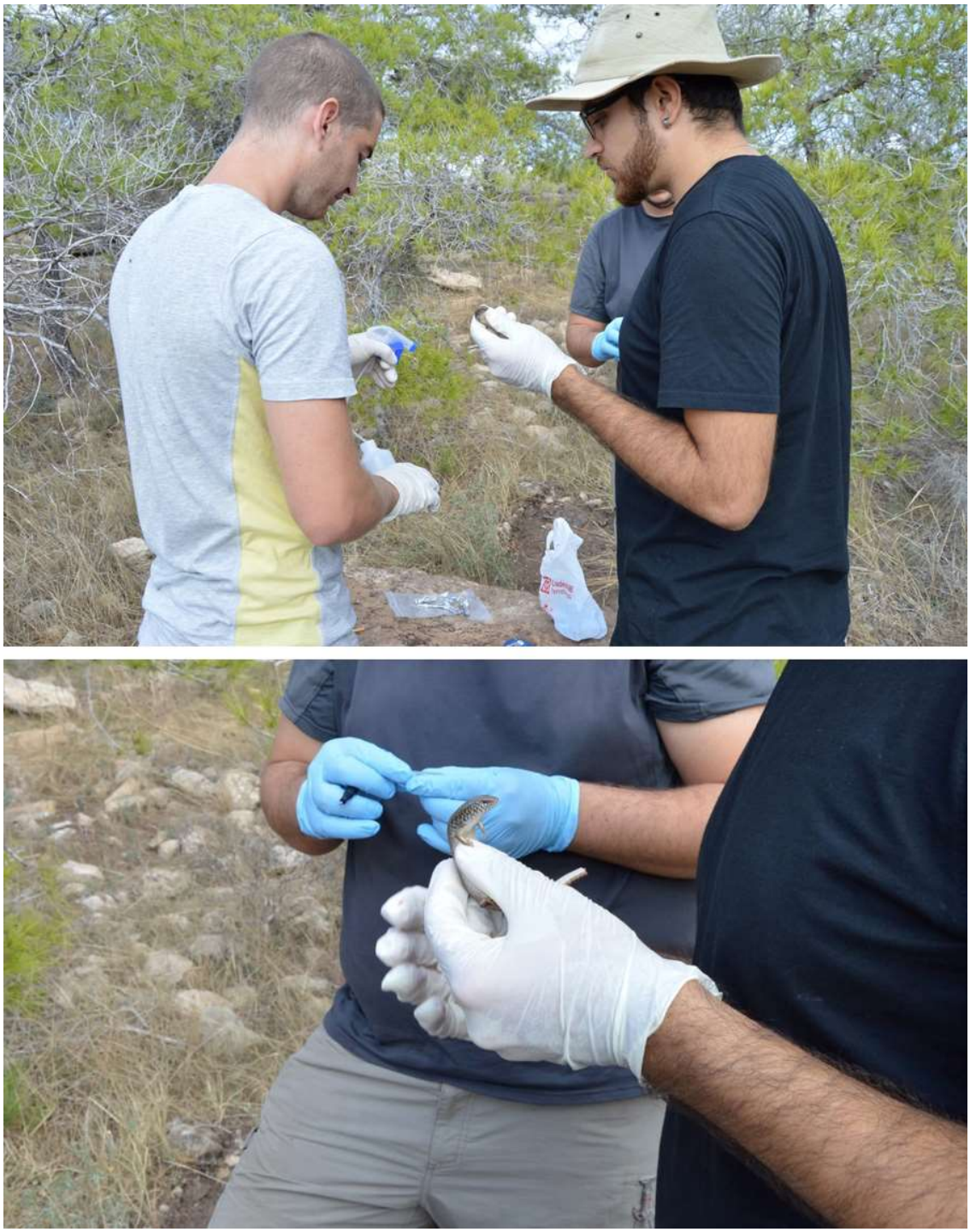

Figure 6.3.- Collection of tissue samples by Miguel Alonso, Rubén Sánchez and the author. Individual CN12645 (♂ n.3), October 2017 [Picture taken by Marcos Real].

Inc.). Chromatographs were checked and the forward and reverse sequence contigs for each sample were assembled and edited using Geneious v.7.1.9 (Biomatter Ltd.). Sequences were aligned using MAFFT v.7.3 (Katoh and Standley, 2013) with default parameters. We translated the final alignment into amino acids and no stop codons were detected.

6.2.2. *Phylogenetic analyses*

Phylogenetic analyses were performed under maximum likelihood (ML) and Bayesian inference (BI) frameworks. The ML analysis was conducted in RAxML v.8.1.2 as implemented in raxmlGUI v.1.5 (Silvestro and Michalak, 2012). The analysis was performed with the GTR+G model of sequence evolution and 100 random addition replicates. Nodal support was assessed with 1,000 bootstrap replicates.

The BI analysis was conducted with BEAST v.1.8.4 (Drummond et al., 2012). We used jModelTest v.2.1.7 (Guindon and Gascuel, 2003; Darriba et al., 2012) to select the best model of nucleotide substitution under the Bayesian information criterion (BIC). We carried out the BEAST analysis with the following priors (otherwise by default): TrN+G model; Coalescent: Constant size tree model; random starting tree; alpha prior uniform (0–10); uncorrelated relaxed clock (uniform distribution; 0–1).

Three individual runs of $2x10^6$ generations were carried out, with sampling at intervals of $2x10^3$ generations. Convergence, posterior trace plots, effective sample sizes (>200), and burn-in were evaluated with Tracer v.1.6 (Rambaut et al., 2014). The tree runs were combined in LogCombiner discarding the first 10% of the trees as burn-in and the ultrametric tree was generated with TreeAnnotator (both available in the BEAST package). Phylogenetic trees were visualized with FigTree v.1.4.3 (Rambaut and Drummond, 2010).

6.3. Results

Between April 2017 and May 2018, 35 individuals of *C. ocellatus* were identified, from which morphometric measurements of 12 distinct individuals could be obtained, all were adults (snout-vent length, SVL > 55 mm, Çiçek et al., 2013) (Table 6.1). The different attested stages of ontogenetic development have allowed verifying the existence of a breeding population, with young and adult individuals, besides the presence of gravid females (Figure 6.2c). The population is distributed at least in a spatial range of 5.2 km^2.

The preliminary taxonomic assignment of Serra del Molar individuals into *C. ocellatus* has been confirmed, following the criteria of Baha El Din (2006) and Carranza et al. (2008): primitive corporal form within the *Chalcides* genus, elongate and cylindrical; black and white dorsal *ocelli*; atrial overture markedly visible, with exposed tympanum; biometric tail/body ratio (tail length divided by distance from snout tip to cloaca) very close to value 1 (average: 1.05, range: 1.14–0.96; Table 1); pentadactyl front limbs with phalangeal formula 2.3.4.4.3; and pentadactyl hind limbs with phalangeal formula 2.3.4.5.3. The animals present the typical body-form and colouration pattern of the subspecies *C. ocellatus ocellatus* (Figure 6.2).

6.3.1. *Phylogenetic structure*

The dataset of the *cytb* gene used in the phylogenetic analyses included 153 sequences of *C. ocellatus* and had a total length of 303 bp: five newly discovered individuals from Spain, 146 sequences

from across the Mediterranean Sea and adjacent regions, and two specimens of *C. montanus* (see Appendices 7 and 8). The ML and BI phylogenetic trees present a structure of three clades within *C. ocellatus* (Figure 6.4; Appendix 8) separated into the eastern, central and western coastal areas of the Mediterranean Sea. Within these clades, a geographic grouping of specimens is apparent, although with an unsupported topology. In both the ML and BI analyses, Serra del Molar individuals are nested within a clade with specimens from the eastern Mediterranean region.

Four of the five Spanish specimens (CN12645, CN13391, CN13434 and CN13435) cluster together with two Egyptian individuals with high support (bootstrap and posterior probability values, 96 and 1, respectively). These Egyptian specimens (c050-FJ980237 and c051- FJ980238; Kornilios et al., 2010) were collected from Ras El Barr, in the Damietta Branch of the eastern Nile Delta. The sequences of these six specimens (Serra del Molar-Spain and Ras El Barr-Egypt) are almost identical, apart from one single mutation in position 159 where the Spanish specimens have an A, whereas the Egyptian specimens have a G.

The fifth Spanish individual (CN12564) has a different phylogenetic position, clustering with samples from Egypt (including four Egyptian specimens that were collected from Ras El Barr, c048-FJ980235, c049-FJ980236, c052-FJ980239 and c053-FJ980240), Somalia, Libya, Yemen, Turkey, Syria, Greece, and Cyprus, although with no support. This specimen's sequence is different from the other Spanish individuals in seven positions (in sites: 60, G *vs.* A; 96, A *vs.* C; 105, T *vs.* C; 129, C *vs.* G;144, T *vs.* C; 204, G *vs.* A; 285, C *vs.* T, respectively).

6.4. Discussion

Two hypotheses have been proposed to explain the origin of the Mediterranean populations of *C. ocellatus*: natural dispersal (maritime, continental or through temporary terrestrial bridges) and human translocations (Lavin and Papenfuss, 2012). The molecular results rule out any scenario of natural colonization of *C. ocellatus* in Serra del Molar: the phylogenetic tree assigned Serra del Molar individuals within subclade A2, distributed across the eastern Mediterranean basin (Kornilios et al., 2010) and exclude their arrival by "rafting" or other natural dispersal by sea from the Tunisian, Algerian or Moroccan coasts, which are the nearest natural populations of ocellated skinks (Martín et al., 2017; Beddek et al., 2018). Additionally, the populations of *C. ocellatus* from these Maghrebian countries belong to other phylogenetic clades (Carranza et al., 2008; Kornilios et al., 2010; Figure 6.4; Appendix 8). Moreover, the extremely low genetic divergence found in the molecular data and the phylogenetic position of the Serra del Molar individuals allow to rule out their spread by land through a continental bridge within a very old palaeogeographic scenario (for example, during the Messinian Salinity Crisis). Therefore, the genetic assignation in the eastern Mediterranean subclade implies that the only reasonable and plausible scenario is the human-mediated translocation.

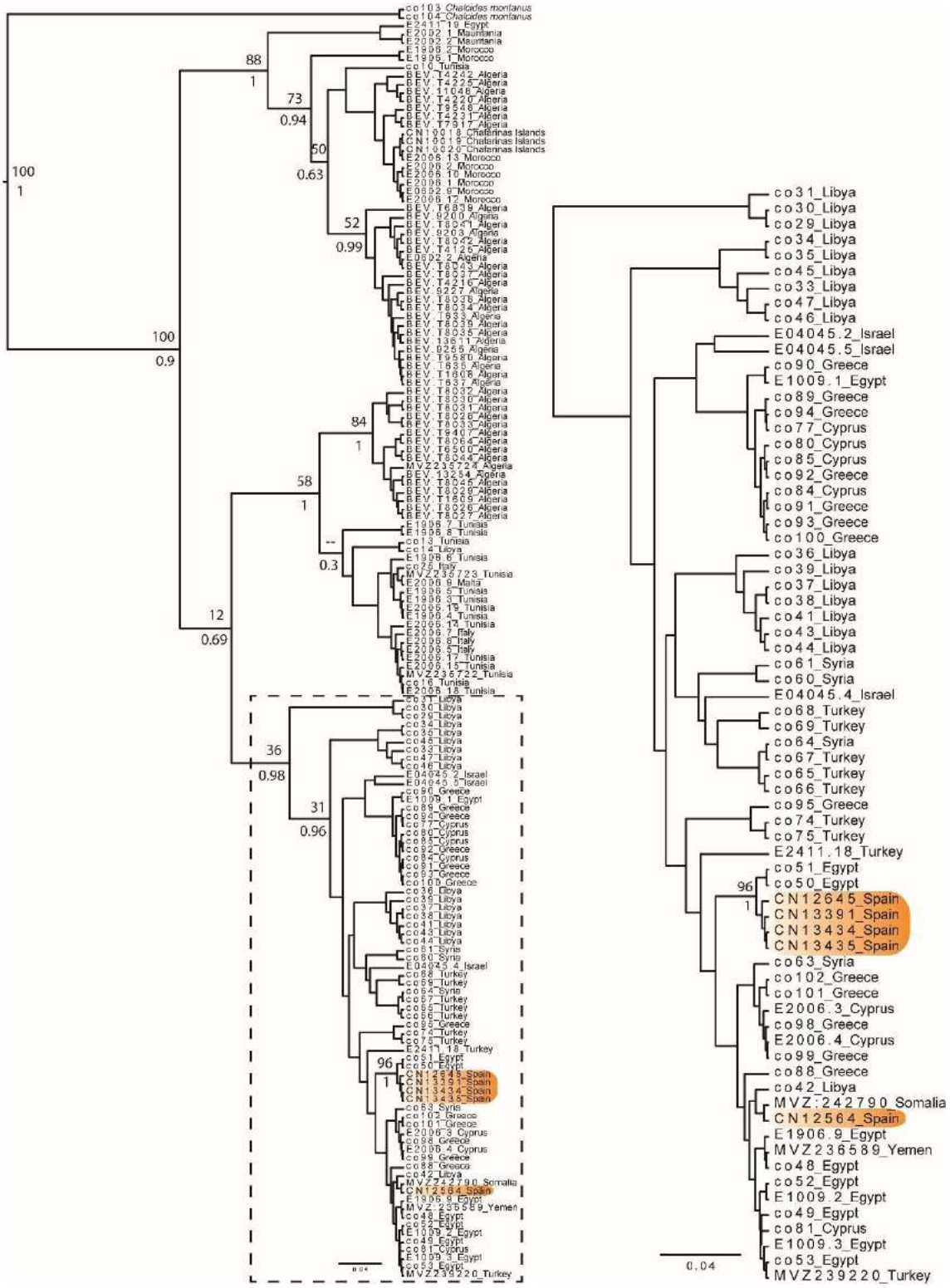

Figure 6.4.- Bayesian Inference Cytochrome *b* phylogenetic tree of *Chalcides ocellatus*. Bootstrap (ML) and Bayesian posterior probabilities (BI) support values are indicated above and below the nodes, respectively. The newly discovered Iberian specimens collected from Serra del Molar are highlighted. Sample codes and localities correlate to specimens in Appendix 7.

The presence of a genetic admixture among the ocellated skinks from Serra del Molar (Figure 6.4, Appendix 8), which has been identified in other human-mediated lizard introductions (Kolbe et al., 2007; Santos et al., 2019), suggests the concurrence of at least two translocation events with distinct sources that originated the new population, or a single introduction with individuals from multiples origins, or that the admixture was already present at the original population or locality, as happens in Ras El Barr.

The dispersal mechanism linked to human activities has been one of the explanations given to the wide distribution of *C. ocellatus* (Schneider, 1981; Anderson, 1999) and is consistent with the phylogenetic studies (Carranza et al., 2008, Kornilios et al., 2010; Lavin and Papenfuss, 2012). In fact, there is a historical record of its introduction into Naples in a shipment of orange trees from Sicily during the 18th century AD (Caputo et al., 1997). Other authors propose different translocation methods, like the use of sand ballasts and their subsequent abandonment in port areas of the Persian Sea (Anderson, 1999). The widespread distribution of the subclade A2 in Kornilios et al. (2010) has been associated with maritime exportation routes of the *Silphium* plant during the Ancient Age (7th-2nd centuries BC), a trade originating in Libyan-Hellenic Cyrenaica (Amigues, 2004), as one of the ways by which *C. ocellatus* expanded through the Eastern Mediterranean (Kornilios et al., 2010).

The regional archaeological record of Serra del Molar has many peculiarities that allow us to postulate the possibility of an introduction due to intra-Mediterranean maritime trade. The surrounding region presents an important archaeological record linked to trade with the Eastern Mediterranean and Phoenician colonization during the second quarter of the 1st millennium BC, associated with the Phoenician colony of La Fonteta (Guardamar del Segura), which is located 2.5 kilometres from Serra del Molar. (González, 2010a, 2010b; Doménech, 2010) (Figure 6.5b). While it was a process that began in the 9th century BC, (Mederos and Ruiz, 2006; García and Prados, 2014), there is previous evidence of previous trade contacts between the Eastern Mediterranean and the southern Valencian Country, such as the Anatolian pottery with Anatolian origin discovered in the Copper/Early Bronze Age settlement of Les Moreres de Crevillent, dated at the 3rd millennium BC (González et al., 1994).

The five sequenced individuals from Serra del Molar belong to the same subclade A2 in Kornilios et al. (2010) and appear to be mainly linked with the Egyptian specimens sampled from Ras El Barr, in the Nile Delta. During the ancient past, in this same area of Lower Egypt were seaports that traded with other regions across the Mediterranean Sea, such as Naukratis, Thonis-Heracleion, Tamiat, Pelusium and Tell el-Ghaba (Stanley et al., 2008; Pfeiffer, 2010; Lupo and Kohen, 2010), all of them were active harbours during the same period as La Fonteta colony (8th–6th centuries BC). In this Phoenician settlement and in nearby contemporary sites, a large amount of Egyptian objects has been discovered together with other manufactures from eastern workshops: a set of six Egyptian scarab amulets, found

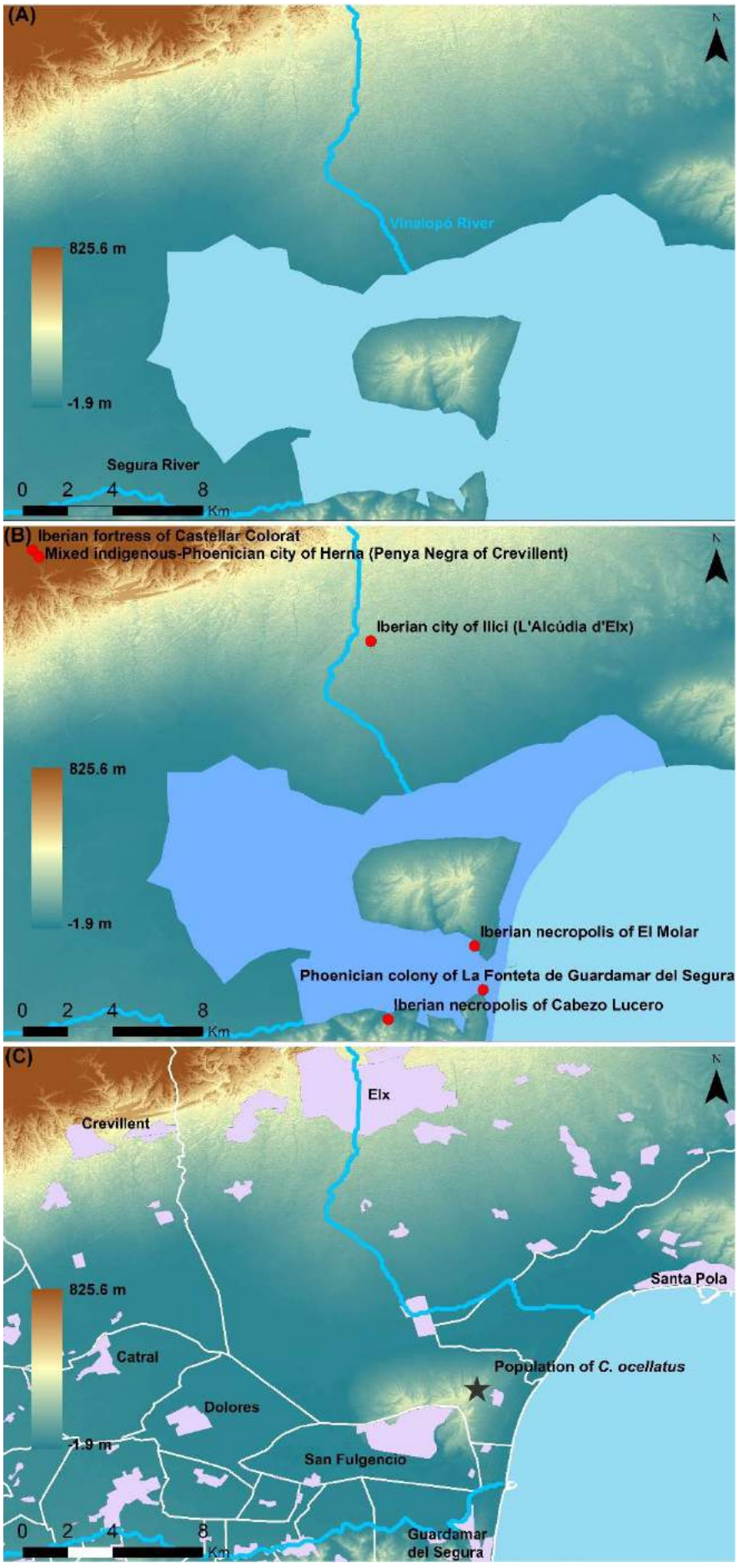

Figure 6.5.- Biogeographical scenario for a Phoenician translocation of *Chalcides ocellatus* into the south-eastern Iberian Peninsula. (A) Serra del Molar as an island, isolated from the mainland by the Mediterranean Sea, during most of the Holocene. (B) Reconstruction of the area during the 8th-6th centuries BC, the formation of a coastal lagoon environment, the position of La Fonteta Phoenician colony and the main findings of objects with Egyptian origin (red point) in the southern Valencian Country. (C) Current situation of Serra del Molar and the current locality of the *Chalcides ocellatus* population (star). *Palaeoenvironmental reconstruction of Serra del Molar during the Holocene to the present is based on Blázquez, (2001); Grau and Moratalla, (2001); Blázquez and Usera, (2010); and Tent-Manclús, (2012).

in various phases of the site (Fonteta II, Fonteta III, Fonteta VI and Fonteta VII-IX, 720 BC to 535 BC) (Escolano, 2012); a faience amulet of the god Bes from Fonteta II and a fragment of an alabaster glass from Fonteta VI (González, 2014). In addition, other objects of Egyptian origin were also found in nearby contemporary sites: the set of scarab amulets of Penya Negra, dated between the end of the 7th century BC at the beginning of the 6th century BC (González, 1976); the two scarab amulets and the aryballos, from the necropolis of El Molar de San Fulgencio, and the ceremonial faience canteen of "New Year", found in tomb no. 18 of the necropolis of Les Casetes de La Vila Joiosa, all of them with a chronology between the 7th-6th centuries BC (Padró, 1975; García and Padró, 2003; García, 2009).

Other objects of origin in the Eastern Mediterranean, possibly in Egypt or elsewhere nearby, have also been found in the regional archaeological record: the Egyptian-style amulet of the cow/*udjat* from Fonteta IV-A, dated between 635- 625 BC (López and Velázquez, 2012); the daemonic mask and the set of four Egyptian-style amulets from the no. 5 tomb of Les Casetes de Vila Joiosa, dated between the 6th-4th centuries BC (García, 2009; Vaquero, 2012); the anepigraphic scarab amulet from Castellar Colorat de Crevillent and the Egyptian-style scarab amulet of green jasper from L'Alcúdia d'Elx (Escolano, 2006); in addition to the dozens of ivory objects and carnelian necklace beads, glass paste and faience found from La Fonteta and Penya Negra (González, 2014; Martínez and Vilaplana, 2014).

A possible route for the ocellated skink translocation is its arrival as an unintentional cargo passenger along with merchandises from Egypt (or another nearby eastern Mediterranean region) to the Phoenician colony of La Fonteta and its later establishment in the periphery of one of its associated Iberian settlements located in Serra del Molar, which was part of its most direct area of influence. The skinks could have arrived inside imported plants or soils, as is proposed by Kornilios et al. (2010) as way for human-mediated dispersals of *C. ocellatus* in the eastern Mediterranean regions, in which the skinks were transported as involuntary stowaways. For example, another agricultural product that could be the transport means for the translocation were eastern varieties of vine strains (*Vitis vinifera*), during the introduction of viticulture in Iberia by the Phoenicians themselves (Buxó, 2008; Iriarte et al., 2016). The molecular data of the conifer *Tetraclinis articulata* from the nearby Sierra de Cartagena (Murcia), which suggest the introduction or local genetic substitution through translocations from Tunisia by the Phoenicians or Carthaginians (Sánchez-Gómez et al., 2013), show the human-mediated mobility of vegetal species across the Mediterranean Sea during this same chronology.

In the context of ancient Mediterranean interactions, similar mechanisms of translocation have been proposed for the colonization of *Vipera aspis hugyi* on the island of Montecristo (Masseti and Zuffi, 2011) and the introduction of *Eryx jaculus* in the Licata region, Sicily (Insacco et al., 2015). The presence of ocellated skinks in this Iberian region, archaeologically linked to the Eastern Mediterranean, reinforces the hypothesis of Kornilios et al. (2010)

about the ancient trade as the main phenomenon for the dispersal of *C. ocellatus*, and reinforces Egypt as the possible main point of the human-mediated translocations.

However, the links between the Iberian south-east with the Eastern Mediterranean, and especially with Egypt, are not limited to the phenomena of Iron Age trade and Phoenician colonization, because the intra-Mediterranean contacts continued during the Roman dominion. More recent historical relations with Egypt occurred during early Middle Age. Singularly, the settling of the *ŷund* (Classical Arabic جند, "army") formed by Islamic troops from Egypt into the Andalusite province or *kora* of *Tudmîr*, which had its epicentre in the Segura river, in the year 743 AD (Gutiérrez, 1996; Vallvé, 1999), the same river that joins the Mediterranean Sea in the southern limit of Serra del Molar. For this region, an evidence of the presence of eastern human populations during the Muslim period are the decorative motifs of Egyptian origin in the Islamic fortified monasteries (*ribats*) of Guardamar del Segura, built on top of the ruins of La Fonteta Phoenician colony (Rubiera, 2004). Another proof of the settlement of Islamic Egyptian groups are some pottery productions that appear in different archaeological sites in the Lower Segura region, which includes Serra del Molar, that show parallelisms with contemporaneous Egyptian productions (Gutiérrez, 1996). The Middle Age manuscripts also relay the existence of direct trade between *Tudmîr*, the adjacent taifa of *Dāniya* (Dénia) and the harbours of the Fatimite Caliphate and Ayyubid Sultanate, particularly the Egyptian port of Alexandria (Azuar, 2016a, 2016b).

One of the most important contributions that the Muslim period had in the southern Valencian area was the introduction of the "oasis crop". Its greatest exponent is the "*Hort de Palmeres d'Elx*" (Palm Grove of Elche), a large monoculture concentration of the date palm (*Phoenix dactylifera*) originated in the 10th century AD that continues at present (Azuar, 1998). During the last decades, palm trees have additionally been used as ornament in private gardens and public parks. This requirement for new trees, which could not be serviced only by local production, was supplied by importing plants from Argentina and Egypt (Berbegal, 2017). Due to the growing demand, the invasive red palm weevil (*Rhynchophorus ferrugineus*) was introduced in Spain mainland through the entry of Egyptian palms without phytosanitary control in 1995 (Ferry and Gómez, 2002). The importation of Egyptian palm trees or another anthropogenic factors (including the current pet trade) may also explain a more recent origin for the translocation and colonization of Serra del Molar. In addition, *C. ocellatus* have demonstrated a high capacity to colonize new areas due to passive dispersals, recently documented in the islands of Stromboli (Italy) and Kasos (Greece) or even in America mainland (Florida and Arizona), where the ocellated skink was absent in thorough herpetological surveys a few years ago (Krysko et al., 2011; Gunn et al., 2012; Lo Cascio and Grita, 2016; Kornilios and Thanou, 2016).

Regardless of the possibility of an introduction during Phoenician times, Islamic period or more recently, the

evolution of the Serra del Molar's environment could explain the survival of an allochthonous population. Although currently it is connected to the continent (Figure 6.5c), in the recent past Serra del Molar was an isolated island in front of the deltas of the Vinalopó and Segura rivers (Figure 6.5a). Recently, the sediments by both rivers settled and filled the area, encircling Serra del Molar to the west and north sides to form a lagoon environment of marshes, swamps and flood plains, which remained with brackish marsh conditions until the 18th century AD (Blázquez, 2001; Grau and Moratalla, 2001; Blázquez and Usera, 2010; Tent-Manclús, 2012) (Figure 6.5b).

This geomorphological evolution, which connects insular areas with continental lands, could function as a "Trojan Horse" for faunal translocations if we add it to the model of human Mediterranean colonization during the first Iron Age. Both Greeks and Phoenicians used peninsulas or small islands in front of the continent to establish their first colonial settlements (Marriner, 2007), usually near the deltas of rivers, whose sedimentary contributions gradually filled the sea coast resulted in the land connection with the insular environments. This happened, for example, in important colonies such as the Greek *Emporion* or the Phoenician *Gadir*, both in the Iberian Peninsula (Tang, 2005; Aubet, 2009). In the case of the translocation of an allochthonous species to one of these insular environments, where it would initially be isolated, the later connection to the continent would create a subsequent scenario that could allow a new expansion of its distribution outside its previous insular range. A two-phases "Trojan Horse" phenomenon that could be added to the interpretive models for intra-Mediterranean translocations.

The preservation of quasi insular conditions until relatively recent times (Figure 6.5c) could have enabled the survival of *C. ocellatus*, in case of an ancient introduction. To date, we were only able to locate individuals of ocellated skink in the north-east quadrant of Serra del Molar, which comparatively has suffered less anthropic impact, although this range may be much larger due to the fossorial cryptic nature of this skink. Most of the area preserve the typical autochthonous scrubs with Aleppo pines and only the lowlands show evidences of old plots, though nowadays are abandoned. Today, the biggest anthropic impact is the massive urbanization, such as estates and roads, in the southern half of Serra del Molar. New faunal surveys will help to clarify and more accurately assess the distribution of *C. ocellatus*, since it is a generalist species, cryptic and adaptable to the presence of humans and agriculture (Schneider, 1981; Schleich et al., 1996).

An alien population of *C. ocellatus* in the Iberian Peninsula raises a new management problem: the possibility of an ancient introduction in Serra del Molar, in addition to the semi-insular character of this area, could be arguments for its conservation. On the other hand, the possible competition with the native skink *Chalcides bedriagai* and the current connectivity with the surrounding regions, may raise arguments to control its population and even propose its eradication. Following the guidelines of the recent review about the status of allochthonous herpetofauna

in Spain and management proposals (Santos et al., 2015), we believe it would be necessary to first carry out field surveys, with monitoring of individuals and experimental studies to assess the *C. ocellatus* interactions with the native biota, specifically the skink *C. bedriagai*, as well as to perform ecological niche models that might hint on the future distribution trends and possible expansion of this species. The results of these proposed studies will help to evaluate the criteria in future management for *C. ocellatus* in Serra del Molar.

6.5. Conclusions

In this study we present the first record for ocellated skink in the Iberian Peninsula, from Serra del Molar (South-east Spain). We combined molecular analyses and archaeological records to study the origin of this population. The molecular results indicate that the population of C. *ocellatus* in Serra del Molar is phylogenetically closely related to specimens from north-eastern Egypt and southern Red Sea. We suggest that the species arrived at the Iberian Peninsula most likely through human-mediated dispersal by using the trade routes. Between the Iron to Middle Ages, even now, the region surrounding Serra del Molar has been the destination of human groups and commercial goods of Egyptian origins, in which *C. ocellatus* could have arrived as stowaways. The regional geomorphological evolution would have restricted its expansion out of Serra del Molar. These findings provide new data about the impact of human movements on faunal introductions and present new information relating to mechanisms of long-distance translocations.

Supplementary data

Appendix 7. Supplementary Table 6.S1.- Specimens used in the genetic analyses and related GenBank accession codes (pages 294-298).

Appendix 8. Supplementary Figure 6.S1.- Cytochrome b Maximum likelihood phylogenetic tree of *Chalcides ocellatus*. Bootstrap (ML) and Bayesian posterior probabilities (BI) support values are indicated above and below the nodes, respectively. The newly discovered Iberian specimens collected from Serra del Molar, Elx are highlighted. Sample codes and localities correlate to specimens in Appendix 7 (page 299).

UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Capítulo 7

Conclusiones globales y perspectivas de futuro

En esta Tesis Doctoral se ha realizado un estudio multidisciplinar de la herpetofauna de los últimos 60.000 años en la Península Ibérica, centrado especialmente en yacimientos arqueo-paleontológicos que abarcan desde las últimas comunidades de *Homo neanderthalensis* musterienses hasta la Edad del Bronce. A través del estudio comparativo por medio de métodos estadísticos, nuestro objetivo consistía en analizar la composición de las especies de anfibios y reptiles, identificando posibles agrupaciones sincrónicas y variaciones diacrónicas, de acuerdo con los ciclos de cambio climático del Pleistoceno Superior y del Holoceno. Al menos 47 taxones diferentes se han identificado a nivel genérico o específico en los 58 yacimientos arqueo-paleontológicos con presencia herpetológica para este periodo. Las asociaciones de herpetofauna fósil y los Análisis de Correspondencia nos han permitido identificar dos grandes regiones bióticas durante el Pleistoceno final (MIS 3 y MIS 2). La primera región biótica está integrada por el centro y sur de la Península Ibérica, con especies termófilas y mediterráneas como las más representativas del registro herpetofaunístico (*Pleurodeles waltl*, *Pelobates cultripes*, *Bufo* gr. *Bufo bufo* = *Bufo spinosus*, *Epidalea calamita*, *Testudo hermanni*, *Timon lepidus*, *Zamenis scalaris*, *Malpolon monspessulanus* y *Vipera latastei*). La segunda gran región biótica comprende la zona atlántico-cantábrica y el noreste ibérico, y se caracteriza por la asociación de especies eurosiberianas y generalistas tolerantes como dominantes en las secuencias prehistóricas (*Alytes* sp., *Bufo* gr. *B. bufo*, *E. calamita*, *Rana temporaria-iberica*, *Anguis fragilis* y *Vipera* sp.), aunque en el área nororiental están acompañadas, en menor medida, por algunas especies tolerantes mediterráneas (*Pelodytes punctatus* y *Coronella girondica*).

Las implicaciones paleoclimáticas de estas grandes asociaciones señalan el mantenimiento de las condiciones típicamente cálidas mediterráneas para las regiones central y meridional, mientras que las zonas septentrional y nororiental presentaban un régimen climático generalmente frío y húmedo dominado por espacios boscosos y praderas húmedas. Los principales cambios biogeográficos se producen tras el inicio de la fase postglacial (MIS 1), con la consiguiente mejora climática que produjo la expansión de las especies termófilas hacia el norte de la Península Ibérica (como *P. cultripes*, *Tarentola mauritanica*, *T. lepidus*, *Z. scalaris* o *M. monspessulanus*), posiblemente aprovechando la existencia de corredores naturales como el Valle del Ebro o la costa atlántica. Paralelamente, nuevas especies europeas (como *Lacerta bilineata*, *Hierophis viridiflavus* y *Zamenis longissimus*) entraron por los márgenes de los Pirineos habiendo pasado por el sur de Francia, procedentes de otros

refugios climáticos más orientales; su expansión pudo haberse detenido en el norte por la colonización contemporánea de especies mediterráneas ibéricas procedentes del sur. Las introducciones de, al menos, cuatro especies de origen magrebí (*Hyla meridionalis*, *Testudo graeca*, *Hemidactylus turcicus* y *Chamaeleo chameleon*), posiblemente causadas por el hombre y datada por los estudios genéticos en tiempos relativamente recientes, representan los procesos más recientes de aparición y expansión de nuevos anfibios y reptiles en la Península Ibérica durante el Holoceno medio-tardío.

Estudios anteriores han reportado que el impacto humano sobre el paisaje ha ido aumentando a lo largo del Holoceno, alterándolo y transformándolo según sus necesidades, especialmente a partir del Neolítico. Este proceso de creciente antropización ambiental comenzó con el aumento de la sedentarización de los grupos de cazadores-recolectores y la difusión de la agricultura y la ganadería. Luego continuó con la progresión de la complejidad y la jerarquización social, que culminó con el surgimiento de las primeras culturas urbanas. Las egagrópilas de los niveles MIR4 y MIR5 de la Cueva de El Mirador (Sierra de Atapuerca, Burgos) se han examinado multidisciplinarmente para evaluar la influencia humana sobre la herpetofauna y el paisaje en un contexto arqueológico con abundantes pruebas de explotación ganadera y agrícola. El objetivo principal es conocer cómo se adaptaron los anfibios y reptiles a los cambios producidos en el paisaje antropizado, deduciendo así sus efectos en la composición herpetofaunística.

Estas veinte tafocenosis de MIR4 y de MIR5, compuestas mayoritariamente por restos de herpetofauna, fueron aportadas al sedimento de la cueva durante una fase de enterramiento humano durante el Calcolítico principios de la Edad de Bronce, lo que permitió su conservación en un contexto muy poco perturbado. El estudio tafonómico de la mayor de las tafocenosis recuperadas (acumulación MIR5-P22-n4, 7,8 x 2,7 x 2,4cm) corroboró su origen coprocenótico. El estudio taxonómico ha identificado al menos doce taxones diferentes, entre los que se encuentran un urodelo (*Triturus marmoratus*), dos anuros (*Hyla* gr. *Hyla arborea* = *Hyla molleri*, y *Rana temporaria*), seis escamosos (*Anguis fragilis*, *Chalcides striatus*, *Lacerta* cf. *bilineata*, *T. lepidus*, *Coronella austriaca* y *Vipera aspis-seoanei*) y dos roedores (Arvicolinae indet, y *Apodemus* cf. *sylvaticus*). Las ranitas de San Antón, *Hyla* gr. *H. arborea* (*H. molleri*), constituyen el 84% de los restos y el 79% de los individuos de la acumulación. Los análisis tafonómicos cuantitativos y cualitativos se han centrado en los huesos de *Hyla* y muestran la presencia de marcas de rotura y digestión asociadas a la depredación animal, aunque en porcentajes bajos y en grados ligeros o moderados. Por sus características, la acumulación de MIR5-P22-n4 se ha identificado como una egagrópila producida por un búho de tamaño medio-grande (categoría 2), como el búho real *Bubo bubo* o el cárabo común *Strix aluco*. La rapaz nocturna habría cazado sus presas durante un período húmedo en primavera, cuando se produce la reproducción de las ranitas de San Antón, mostrando una posible

evidencia de una depredación oportunista sobre un recurso estacional.

Las asociaciones de pequeños vertebrados de las acumulaciones de El Mirador son muy diversas e incluyen por lo menos 350 individuos de 20 taxones diferentes, entre ellos dos urodelos (*Lissotriton helveticus* y *T. marmoratus*), seis anuros (*Alytes obstetricans*, *P. cultripes*, *Hyla* gr. *H. arborea = H. molleri*, *E. calamita*, *Bufo* gr. *B. bufo = B. spinosus*, y *R. temporaria*), seis escamosas (*A. fragilis*, *C. striatus*, *Lacerta* cf. *bilineata*, *T. lepidus*, *C. austriaca* y *V. aspis/seoanei*), aves indeterminadas (Aves indet.), una musaraña (*Sorex araneus*) y cuatro roedores (*Microtus agrestis*, *Microtus arvalis*, *Terricola duodecimcostatus* y *A. sylvaticus*). El estudio comparativo de las acumulaciones de MIR4 y MIR5, interpretadas como egagrópilas o parte de ellas, sugiere la existencia de variaciones estacionales en la composición de la dieta del agente acumulador. Los Análisis de Correspondencia han separado en dos grupos los conjuntos de egagrópilas de MIR4 debido a su diferente composición (grupo MIR4.A y grupo MIR4.B), mientras que no han mostrado diferencias significativas para MIR5. A través de la etología, la fenología, la actividad anual y los ciclos reproductivos de las presas documentadas, se postula la existencia de un factor estacional determinante, debido a la influencia del fin de la hibernación y los ciclos reproductivos en los anfibios y reptiles. En las egagrópilas del MIR4 hay una doble estacionalidad, representada por los dos grupos separados en los Análisis de Correspondencia. El grupo MIR4.A está compuesto principalmente por anfibios, con sus ciclo reproductivos y mayor actividad después de la hibernación y durante las primeras semanas de la primavera. El segundo grupo, MIR4.B, está integrado principalmente por reptiles y así como también por especies de influencia mediterránea. Por este motivo, MIR4.B se sitúa entre mediados de la primavera y el verano, cuando los reptiles se reproducen y cuando las especies más termófilas comienzan su actividad anual. En cambio, las egagrópilas de MIR5 están monopolizadas por *Hyla* gr. *H. arborea* (*H. molleri*), que se reproduce masivamente en grandes aglomeraciones de individuos durante la fase húmeda de mediados de la primavera.

La composición taxonómica y el número de presas en las egagrópilas de MIR4 y MIR5 son muy inusuales y no tienen paralelo en la literatura contemporánea. Los datos modernos también sugieren que el impacto humano puede causar cambios en la dieta de las rapaces nocturnas, como una adaptación a la presión que sufren debido a la antropización ambiental. Los datos arqueobotánicos y el registro de pequeños mamíferos de El Mirador apoyan la hipótesis del impacto humano como factor condicionante del depredador en el entorno de la Sierra de Atapuerca. Posiblemente en ausencia o escasez de presas más óptimas, el depredador (potencialmente *B. bubo* según los datos tafonómicos anteriores y la actividad diaria de las presas cazadas) optó por otras presas menos óptimas pero más abundantes en el entorno, especialmente durante sus fases reproductivas de acuerdo con los ciclos estacionales.

La reconstrucción paleoambiental a través de las diferentes agrupaciones estacionales muestra cambios en la distribución de los principales hábitats, con aumentos en las zonas húmedas entre finales del invierno y mediados de la primavera, así como un incremento de la sequedad entre mediados de la primavera y el verano. Las reconstrucciones paleoclimáticas para MIR4 y MIR5 exhiben un clima muy similar al actual pero ligeramente más húmedo. Los cálculos separados según criterios estacionales no mostraron diferencias significativas en las temperaturas anuales y mensuales, aunque sí aumentos de las precipitaciones en el grupo MIR4.A, asignado al invierno-mediados de la primavera. La comparación con el registro de pequeños mamíferos de MIR4 y MIR5 muestra una alta coincidencia en la reconstrucción paleoclimática pero mayores discrepancias en la interpretación paleoambiental. Aunque el registro de las egagrópilas de la Cueva de El Mirador es excepcional en comparación con el escenario habitual en los yacimientos kársticos, los nuevos datos proporcionados en esta tesis doctoral exhortan el uso combinado de las asociaciones de microfauna vertebrada para un mayor grado de confianza en las reconstrucciones e interpretaciones del pasado.

La inclusión de las asociaciones herpetofaunísticas de las egagrópilas de MIR4 y MIR5 en el contexto del norte de la Península Ibérica durante el Cuaternario Final ha demostrado su vinculación con el proceso de expansión posglacial. Sus composiciones son una mezcla de especies generalistas y eurosiberianas, higrófilas y termófilas mediterráneas. La situación geográfica de la Sierra de Atapuerca, en un corredor natural entre la cuenca del Duero y el valle del Ebro, y entre el Sistema Ibérico y la Cordillera Cantábrica, habría posibilitado la llegada de especies de múltiples orígenes biogeográficos durante el Holoceno. La comparación con las anteriores asociaciones herpetofaunísticas de El Portalón y con la herpetofauna actual indica una evolución desde una herpetofauna con afinidades eurosiberianas y de contextos climáticos fríos hasta la situación actual, en la que predominan las especies termófilas mediterráneas propias de condiciones más cálidas. La herpetofauna de las egagrópilas muestra una fase intermedia, compartiendo especies eurosiberianas, hidro-higrófilas y termófilas mediterráneas. En el futuro, los nuevos trabajos que completen la secuencia de El Mirador nos darán la oportunidad de estudiar con mayor detalle la evolución de las comunidades de herpetofauna y los procesos de cambio a largo plazo a nivel local.

Otro objetivo de esta tesis doctoral es documentar los impactos humanos durante el Holoceno en las comunidades herpetofaunísticas de la Península Ibérica en relación con la introducción de nuevas especies. Los datos recogidos por el análisis paleobiogeográfico sugieren la posible conexión entre la llegada de especies norteafricanas a la Península Ibérica y los movimientos humanos provenientes de las costas del sur del Mediterráneo durante el Holoceno, singularmente desde el Magreb según los estudios moleculares. Estudios anteriores ya han relacionado el comercio antiguo marítimo y los movimientos de personas

y mercancías con la posible introducción, intencionada o no, de herpetofauna y de otros pequeños vertebrados terrestres entre diferentes regiones de la cuenca mediterránea.

En esta tesis doctoral presentamos el primer registro de una población de eslizón ocelado *Chalcides ocellatus* para la Península Ibérica, de la Sierra del Molar (Alicante). El eslizón ocelado tiene distribución natural que cubre casi toda la cuenca mediterránea, Asia suroccidental y el noreste africano. Se han propuesto dos hipótesis para explicar su amplia difusión: las dispersiones naturales y las translocaciones humanas. Los datos moleculares publicados anteriormente sugieren la existencia de un fenómeno de dispersión reciente en el Mar Mediterráneo. Hemos combinado los análisis moleculares y los registros arqueológicos para estudiar el origen de la nueva población. Los resultados moleculares indican que los *C. ocellatus* en la Sierra del Molar están filogenéticamente relacionados de manera muy próxima con los especímenes del nordeste de Egipto y el sur del Mar Rojo. Sugerimos que la especie llegó a la Península Ibérica muy probablemente a través de una dispersión mediada por el hombre, utilizando las rutas comerciales. Entre la Edad del Hierro y la Edad Media, incluso ahora, la región que rodea la Sierra del Molar ha sido el destino de grupos humanos y mercancías comerciales de origen egipcio, a las que *C. ocellatus* podría haber llegado como polizón. La evolución geomorfológica regional habría restringido su expansión fuera de la Sierra del Molar, debido a las condiciones insulares de la zona hasta tiempos muy recientes. Estos hallazgos proporcionan nuevos datos sobre el impacto de los movimientos humanos en las introducciones de la fauna y aportan nueva información relativa a los mecanismos de las translocaciones a larga distancia.

Por último, se necesitan nuevos esfuerzos en los estudios herpetológicos para los contextos arqueológicos de las regiones mediterráneas ibéricas. Los datos conocidos actualmente muestran que los primeros registros de algunas especies magrebíes en la Península Ibérica están datados en cronologías recientes, durante el Holoceno medio-tardío, coincidiendo con el inicio de las migraciones humanas y los contactos a larga distancia (colonización humana de las islas mediterráneas, comercio de la Edad del Cobre y Bronce, más tarde griegos y fenicios). La Paleo/Arqueo-Herpetología puede ayudarnos a identificar su llegada su relación con el factor humano.

Chapter 7

Global conclusions and future perspectives

In this doctoral thesis, a multidisciplinary study of the herpetofauna from the last 60,000 years in the Iberian Peninsula has been performed, focusing specially on archaeo-palaeontological sites ranging from the last Mousterian communities of *Homo neanderthalensis* to the Bronze Age. Through the comparative study by statistical methods, our aim has been to analyze the composition of amphibian and reptile associations, identifying possible synchronic groups and diachronic variations, according to the climate change cycles of the Late Pleistocene and the Holocene. At least 47 different taxa have been identified at generic and specific level in all 58 Iberian archaeo-palaeontological sites with a herpetofaunal presence from this period. The fossil herpetofaunal assemblages and the Correspondence Analyses have allowed us to establish two major biotic regions during the latest Pleistocene (MIS 3 and MIS 2). The first biotic region is formed by the center and south of the Iberian Peninsula, with thermophilic and Mediterranean species as the most representative ones of the herpetofaunal record (*Pleurodeles waltl*, *Pelobates cultripes*, *Bufo* gr. *Bufo bufo* = *Bufo spinosus*, *Epidalea calamita*, *Testudo hermanni*, *Timon lepidus*, *Zamenis scalaris*, *Malpolon monspessulanus* and *Vipera latastei*). The second major biotic region comprises the Atlantic-Cantabrian facade and northeastern Iberia, and is characterized by the association of Eurosiberian and tolerant generalist taxa as the dominant species of the prehistoric sequences (*Alytes* sp., *Bufo* gr. *B. bufo*, *E. calamita*, *Rana temporaria-iberica, Anguis fragilis* and *Vipera* sp.), although in the northeastern area they are accompanied, to a lesser extent, by some tolerant Mediterranean species (*Pelodytes punctatus* and *Coronella girondica*).

The palaeoclimatic implications of these large associations indicate the maintenance of typically warm Mediterranean conditions in the central and southern regions, while the northern and northeastern areas present a generally cold and humid climatic regime dominated by wooded spaces and wet meadows. The main biogeographic changes occur after the beginning of the postglacial phase (MIS 1), with the resulting climate improvement that produced the expansion of the thermophilic species towards the north of the Iberian Peninsula (as *P. cultripes*, *Tarentola mauritanica*, *T. lepidus*, *Z. scalaris* or *M. monspessulanus*), possibly taking advantage of the existence of natural corridors such as the Ebro Valley or the Atlantic coast. In parallel, newcomer European species (as *Lacerta bilineata*, *Hierophis viridiflavus* y *Zamenis longissimus*) entered via the Pyrenean margins having passed through southern France, coming from other more eastern climatic refuges; their expansions may have been halted in the north by the

contemporaneous colonization of Iberian Mediterranean species from the south. The introduction of at least four Maghrebian species (*Hyla meridionalis*, *Testudo graeca*, *Hemidactylus turcicus* and *Chamaeleo chameleon*), possibly caused by humans and dated by genetic studies to relatively recent times, represents the most recent processes of emergence and expansion of new amphibians and reptiles in the Iberian Peninsula during the Middle-Late Holocene.

Previous studies have reported that the human impact on the landscape has been increasing throughout the Holocene, altering and transforming it according to its necessities, notably since the Neolithic. This process of increasing environmental anthropization began with the increase in sedentarization of hunter-gatherer groups and the spread of agriculture and livestock. It then continued with the progression of social complexity and hierarchization that culminated in the emergence of the first urban cultures. The small vertebrate accumulations from levels MIR4 and MIR5 of El Mirador cave (Sierra de Atapuerca, Burgos) have been examined multidisciplinary to evaluate the human influence on herpetofauna and landscape in an archaeological context with abundant evidence of livestock and agricultural exploitation. The main objective is to know how the amphibians and reptiles adapted to the changes produced in the anthropized landscape, thus inferring its effects on the herpetofaunal composition.

These twenty taphocenoses from MIR4 and MIR5, composed mainly by herpetofaunal remains, were contributed to the karstic sediment during a human burial phase during the Chalcolithic and early Bronze Ages, which allowed their conservation in a very slightly disturbed context. The taphonomic study of the largest of the recovered taphocenosis (MIR5-P22-n4 accumulation, 7.8x2.7x2.4cm) corroborated its coprocenotic origin. The taxonomical study has identified at least 12 different taxa, which include one urodele (*Triturus marmoratus*), two anurans (*Hyla* gr. *Hyla arborea* = *Hyla molleri*, and *Rana temporaria*), six squamates (*Anguis fragilis*, *Chalcides striatus*, *Lacerta* cf. *bilineata*, *T. lepidus*, *Coronella austriaca* and *Vipera aspis*/*seoanei*), and two rodents (Arvicolinae indet, and *Apodemus* cf. *sylvaticus*). Tree frogs, *Hyla* gr. *H. arborea* (*Hyla molleri*), constitute 84% of the remains and 79% of the individuals in the accumulation. Quantitative and qualitative taphonomic analyses are focused on *Hyla* bones and show the presence of breakage and digestion marks associated with animal predation, albeit in low percentages and in light or moderate degrees. Due to its characteristics, MIR5-P22-n4 accumulation has been identified as a pellet accumulation produced by a medium-large owl (category 2), as the eagle-owl *Bubo bubo* or the tawny owl *Strix aluco*. The nocturnal raptor hunted its preys during a wet period in spring, when the reproduction of the Iberian tree frogs occurs, showing a possible evidence of opportunistic predation on a seasonal resource.

The associations of small vertebrates from El Mirador accumulations are very diverse and include at least 350 individuals of 20 different taxa, including two urodeles

(*Lissotriton helveticus* and *T. marmoratus*), six anurans (*Alytes obstetricans*, *P. cultripes*, *Hyla* gr. *H. arborea* = *H. molleri*, *E. calamita*, *Bufo* gr. *B. bufo* = *B. spinosus*, and *R. temporaria*), six squamates (*A. fragilis*, *C. striatus*, *Lacerta* cf. *bilineata*, *T. lepidus*, *C. austriaca* and *V. aspis*/*seoanei*), indeterminate birds (Aves indet.), one shrew (*Sorex araneus*), and four rodents (*Microtus agrestis*, *Microtus arvalis*, *Terricola duodecimcostatus* and *A. sylvaticus*). The comparative study of the accumulations of MIR4 and MIR5, interpreted as pellets or part of them, suggests the existence of seasonal variations in the diet composition of the accumulating agent. Correspondence Analysis has separated the pellet sample of MIR4 into two groups due to their different composition (group MIR4.A and group MIR4.B), while showing no significant differences for MIR5. Through the ethology, phenology, annual activity and reproductive cycles of the documented preys, the existence of a determining seasonal factor is postulated, due to the influence of the end of hibernation and the reproductive cycles of amphibians and reptiles. In MIR4 pellets there is a double seasonality, represented by the two groups separated by Correspondence Analyses. The MIR4.A group is mainly composed of amphibians, with a reproductive cycle and increased activity after hibernation and during the first weeks of spring. The second group, MIR4.B, is integrated mainly by reptiles and also by species of Mediterranean influence. For this reason, MIR4.B is situated in a period between mid-spring and summer, when reptiles reproduce and when the most thermophilic species begin their annual activity. In contrast, MIR5 is monopolized by *Hyla* gr. *H. arborea* (*H. molleri*), which reproduces massively in large agglomerations during the mid-spring wet phase.

The taxonomic composition and number of preys in pellets from MIR4 and MIR5 are very unusual and have no parallel in contemporary literature. Modern data also suggest that human impact may cause changes in the diet of nocturnal raptor, as an adaptation to the pressure they suffer due to environmental anthropization. Archaeobotanical data and the record of small-mammals from El Mirador support the hypothesis of human impact as a conditioning factor for the predator in the Sierra de Atapuerca environment. Possibly in the absence or scarcity of more optimal preys, the predator (potentially *B. bubo* according to the previous taphonomic data and daily activity of the hunted preys) opted for other less optimal but more abundant preys in the surroundings, specially during their reproductive phases in accordance with seasonal cycles.

Palaeoenvironmental reconstruction through the different seasonal associations show changes in the distribution of the main habitats, with increases in wet areas between late winter and mid-spring, as well as an increment in dryness between mid-spring and summer. The palaeoclimatic reconstructions for MIR4 and MIR5 exhibit a climate very similar to the current one but slightly wetter. The separated calculations according seasonal criteria did not show significant differences in annual and monthly temperatures, although there were

increases in precipitation in the group MIR4.A, assigned to winter–mid-spring. The comparison with the record of small-mammals in MIR4 and MIR5 shows a high coincidence in the palaeoclimatic reconstruction but greater discrepancies in the palaeoenvironmental interpretation. Although the record of pellets from El Mirador cave is exceptional in comparison with the usual scenario in karst sites, the new data provided in this doctoral thesis exhort the combined use of microfaunal vertebrate associations for a higher confidence degree in the reconstructions and interpretations of the past.

The inclusion of the herpetofaunal associations of the pellets of MIR4 and MIR5 in the context of the north of the Iberian Peninsula during the Latest Quaternary has shown their link with the process of post-glacial colonization. Their compositions are a mixture of generalist and Eurosiberian taxa, hygrophilous and Mediterranean thermophilic species. The geographical location of the Sierra de Atapuerca, in a natural corridor between the Duero River Basin and the Ebro Valley, and between the Iberian Mountain System and the Cantabrian Mountains, would have made possible the arrival of species of multiple biogeographical origins during the Holocene. A comparison with the previous herpetofaunal associations from El Portalón and with the current herpetofauna indicates an evolution from a herpetofauna with Eurosiberian affinities and cold-climate contexts to the current situation, in which warmer Mediterranean thermophilic species predominate. The herpetofauna of the pellets of MIR4 and MIR5 shows an intermediate phase, sharing Eurosiberian, hydro-hygrophilous and Mediterranean thermophilic species. In the future, new works that complete the sequence of El Mirador will provide us with the opportunity to study with greater detail the evolution of herpetofauna communities and the processes of long-term change locally.

Another objective of this doctoral thesis is to document the human impacts during the Holocene on the herpetofaunal communities of the Iberian Peninsula concerning the introduction of new species. The data collected by the palaeobiogeographic analysis suggest the possible connection between the arrival of North African species to the Iberian Peninsula and human movements from the southern Mediterranean coasts during the Holocene, singularly from the Maghreb according to molecular studies. Previous studies have already connected ancient maritime trade and movements of people and goods to the possible introduction, intentional or not, of herpetofaunal and other small terrestrial vertebrates among different regions of the Mediterranean Basin.

In this doctoral thesis we present the first record of ocellated skink *Chalcides ocellatus* for the Iberian Peninsula, from Serra del Molar (Alacant/Alicante). The ocellated skink has a natural distribution that covers almost the entire Mediterranean Basin, south-western Asia and north-eastern Africa. Two hypotheses have been proposed to explain its widespread dispersion: natural dispersals and human translocations. Previous molecular data suggest the occurrence of a recent dispersal phenomenon across the

Mediterranean Sea. We combined molecular analyses and archaeological records to study the origin of this new population. The molecular results indicate that the *C. ocellatus* in Serra del Molar is phylogenetically closely related to specimens from north-eastern Egypt and southern Red Sea. We suggest that the species arrived at the Iberian Peninsula most likely through human-mediated dispersal by using the trade routes. Between the Iron to Middle Ages, even now, the region surrounding Serra del Molar has been the destination of human groups and commercial goods of Egyptian origins, in which *C. ocellatus* could have arrived as stowaways. The regional geomorphological evolution would have restricted its expansion out of Serra del Molar, due to the insular conditions of the area until very recent times. These findings provide new data about the impact of human movements on faunal introductions and present new information relating to mechanisms of long-distance translocations.

Finally, new efforts are needed in the herpetological studies for archaeological contexts from the Iberian Mediterranean regions. The currently known data show that the first records of some Maghrebian species in the Iberian Peninsula are dated in recent chronology, during the Middle-Late Holocene, coinciding with the beginning of human migrations and long-distance contacts (human colonization of the Mediterranean islands, Chalcolithic and Bronze Age trade, later Greeks and Phoenicians). Palaeo/Archaeo-Herpetology can help us to identify their arrival and their connection with the human factor.

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UNIVERSITAT ROVIRA I VIRGILI
BIOGEOGRAFÍA E IMPACTO HUMANO EN LAS COMUNIDADES DE ANFIBIOS Y REPTILES DEL CUATERNARIO FINAL EN LA PENÍNSULA IBÉRICA: LA CUEVA DEL MIRADOR (ATAPUERCA, BURGOS) Y LA POBLACIÓN DE CHALCIDES OCELLATUS (SCINCIDAE) DE LA SERRA DEL MOLAR (ALICANTE)
José Francisco Bisbal Chinesta

Appendix 1 - Data matrix for northern region

	Rana temporaria-iberica	*Anguis fragilis*	*Bufo gr. Bufo bufo*	*Alytes*	*Salamandra salamandra*	*Epidalea calamita*	*Lacerta*	*Coronella austriaca*	*Natrix maura*	*Natrix natrix* s.l.	*Hyla*	*Malpolon monspessulanus*	*Chioglossa lusitanica*	*Discoglossus galganoi*	*Chalcides striatus*	*Timon lepidus*	*Mesotriton alpestris*	*Lissotriton helveticus*	*Triturus marmoratus*	*Coronella girondica*	*Zamenis longissimus*	*Hierophis viridiflavus*	*Vipera*	*Zamenis scalaris*
ASKONDO N.13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASKONDO N.1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CONDE N104	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CONDE N103	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CONDE N10b	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CONDE N20a	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CONDE N2a1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CONDE N2a2	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COBRANTE N.7	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COBRANTE N.6	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COBRANTE N.5	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COBRANTE N.4	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COBRANTE N.3	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COBRANTE N.2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COBRANTE N.1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EIRÓS 3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
EIRÓS 2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
PORTALÓN P16	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P15	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P14	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P13	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P12	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P11	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P10	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
PORTALÓN P9	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
PORTALÓN P8	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
PORTALÓN P7	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
PORTALÓN P6	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P5	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P4	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P3	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PORTALÓN P2	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Rana temporaria-iberica	*Anguis fragilis*	*Bufo gr. Bufo bufo*	*Alytes*	*Salamandra salamandra*	*Epidalea calamita*	*Lacerta*	*Coronella austriaca*	*Natrix maura*	*Natrix natrix s.l.*	*Hyla sp-*	*Malpolon monspessulanus*	*Chioglossa lusitanica*	*Discoglossus galganoi*	*Chalcides striatus*	*Timon lepidus*	*Mesotriton alpestris*	*Lissotriton helveticus*	*Triturus marmoratus*	*Coronella girondica*	*Zamenis longissimus*	*Hierophis viridiflavus*	*Vipera sp-*	*Zamenis scalaris*
PORTALÓN P1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANTOLIÑAKO N.D	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANTOLIÑAKO N.C	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANTOLIÑAKO N.B	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANTOLIÑAKO N.A	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SANTIMAMIÑE Arg-o	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SANTIMAMIÑE Camr	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
SANTIMAMIÑE Csn	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
SANTIMAMIÑE Balm	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SANTIMAMIÑE Almp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SANTIMAMIÑE Slnc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SANTIMAMIÑE Arcp	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SANTIMAMIÑE Slm	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SANTIMAMIÑE Lsm	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
ERRALLA N.VI	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERRALLA N.V	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERRALLA N.IV	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERRALLA N.III	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERRALLA N.II	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VALDAVARA-1 N.2	1	1	1	0	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0
VALDAVARA-1 N.1	1	1	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0
CATALINA N.III	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
CATALINA N.II	1	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0
CATALINA N.I	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1	0
LAMINAK II N.II-I	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
AIZKOLTZO LL.15-12	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0
MIRÓN 10	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MIRÓN 9	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
MIRÓN 8	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MIRÓN 7	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MIRÓN 6	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MIRÓN 5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MIRÓN 4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
MIRÓN 3	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LAS ORCILLAS-1 C.II-I	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1
PEÑA LARGA N.IV-I	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERREKATXUETAKO ATXA	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Supplementary Table 1.S1.- Data matrix of the northern region with significative herpetofaunal assemblages from the latest Pleistocene to the Late Holocene.

Appendix 2 - Data matrix for north-eastern region

	Rana temporaria	*Anguis fragilis*	*Bufo gr. Bufo bufo*	*Alytes obstetricans*	*Salamandra salamandra*	*Epidalea calamita*	*Coronella austriaca*	*Natrix maura*	*Coronella girondica*	*Malpolon monspessulanus*	*Pelodytes punctatus*	*Vipera aspis*	*Pelobates cultripes*	*Calotriton asper*	*Zamenis scalaris*	*Timon lepidus*	*Vipera latastei*
GEGANT IV	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0
GEGANT V	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GEGANT III	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
TEIXONERES IIB	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0
TEIXONERES N.II	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0
ABRIC ROMANÍ N.O	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ABRIC ROMANÍ N.K	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ABRIC ROMANÍ N.J	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ABRIC ROMANÍ N.E	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
ABRIC ROMANÍ N.D	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
XARAGALLS C8	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0
XARAGALLS C7	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0
XARAGALLS C6	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1
XARAGALLS C5	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
XARAGALLS C4	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1
XARAGALLS C3	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
CANYARS	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0
GALLS CARBONERS N.108-105	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
COLOMERA CE15	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
COLOMERA CE14-13	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0
COLOMERA CE12	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0
COLOMERA EE1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BALSA LA TAMARIZ	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	0

Supplementary Table 1.S2.- Data matrix of the north-eastern region with significative herpetofaunal assemblages from the latest Pleistocene to the Late Holocene.

Appendix 3 - Data matrix for southern and central regions

	Bufo gr. Bufo bufo	*Alytes*	*Epidalea calamita*	*Coronella austriaca*	*Natrix maura*	*Natrix natrix* s.l.	*Malpolon monspessulanus*	*Discoglossus galganoi*	*Chalcides striatus*	*Timon lepidus*	*Coronella girondica*	*Pelodytes punctatus*	*Pelobates cultripes*	*Zamenis scalaris*	*Tarentola mauritanica*	*Pelophylax perezi*	*Testudo hermanni*	*Pleurodeles waltl*	*Emys orbicularis*	*Macroprotodon brevis*	*Chalcides bedriagai*	*Blanus cinereus*	*Acanthodactylus erythrurus*	*Triturus pygmaeus*	*Hemorrhois hippocrepis*	*Psammodromus algirus*	*Vipera latastei*	*Mauremys leprosa*	*Salamandra salamandra*
CHIMENEAS																													
MALTRAVIESO N.A	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
ESTEBANVELA N.VI	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ESTEBANVELA N.IV	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ESTEBANVELA N.III	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ESTEBANVELA N.II	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ESTEBANVELA N.I	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
VENTANA N.3-4	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
VENTANA N.14-18-24	1	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VENTANA N.7-9-16-22-26	1	1	1	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
SIMA ABRAHAM D11	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BOQUETE DE ZAFARRAYA	1	0	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	0	0
GORHAM N.IV	1	0	1	0	1	0	0	0	0	1	1	0	1	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0	0
GORHAM N.IIIb	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	0	1	1	0	1	1	0	1	1	1	0	1	0	0
GORHAM N.IIIa	1	0	1	0	1	1	1	0	1	1	1	0	1	1	1	0	0	1	0	0	0	0	1	1	1	0	1	0	0
ABRIC SALT X	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
TORREJONES	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
LLOMA BETXÍ	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CASTILLEJO DEL BONETE	1	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
FIGUEIRA BRAVA	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1
NOVA DA COLUMBEIRA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
CALDEIRÂO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
GUIA	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0

Supplementary Table 1.S3.- Data matrix of the central and southern regions with significative herpetofaunal assemblages from the latest Pleistocene to the Late Holocene.

Appendix 4 - Descripción sistemática – Herpetofauna egagrópilas

Métodos

La asignación sistemática de los restos óseos se hizo de acuerdo con los criterios de determinación osteológica establecidos por Augé, (2005), Bailon (1991, 1999), Barahona, (1996), Barahona y Barbadillo (1997), Blain (2005, 2009), Blain y Arribas (2017), Buckley y Sanchiz, (2012), Caputo (2004), Estes et al. (1988), Gleed-Owen, (1998), Holman (1992, 1998), Holmann y Stuart, (1991), Ratnikov, (2015) y Szyndlar, (1984).

Para una observación directa de las características osteológicas, se han consultado especímenes actuales de las colecciones del Museo Nacional de Ciencias Naturales de Madrid (MNCN) y del Laboratorio de Anatomía Comparada del Museo Nacional de Historia Natural de París (MNHN), así como de la colección osteológica propia del Institut Català de Paleoecologia Humana i Evolució Social (IPHES). En lo que respecta a la nomenclatura anatómica, hemos optado por utilizar principalmente los términos en castellano establecidos por Bailón (1986), o en su defecto, la traducción al castellano a partir del francés en Bailón (1999) y Blain (2009), y del inglés a partir de Szyndlar (1984). Para la nomenclatura taxonómica actualizada de la herpetofauna ibérica nos hemos basado en la Lista Patrón de la Asociación Herpetológica Española, publicada por Carretero et al. (2018).

Todas las mediciones se hicieron con un calibre Digital Mitutoyo, 0-6"/0-150mm, con una precisión de 0.01 mm. Las fotografías de los elementos Se realizaron mediante una cámara digital con sensor CMOS de 5Mp CMEX-5 Euromex DC.5000C, acoplada a un microscopio estereoscópico trinocular Euromex Zoom Nexius Zoom NZ.1903-S.

Orden CAUDATA Scopoli, 1777

Familia Salamandridae Goldfuss, 1820

Género *Lissotriton* Bell, 1839

Lissotriton helveticus (Razoumovsky, 1789)

Figura 4.3.A-D

Material examinado:

— MIR4-Q21-n227: 1 escápula-coracoides izquierdo, 1 húmero derecho.

— MIR4-Q21-n228: 3 vértebras dorsales, 2 vértebras caudales.

— MIR4-Q21-n235: 1 húmero derecho.

— MIR4-P21-n246: 1 húmero izquierdo, 4 vértebras dorsales, 1 vértebra caudal.

— MIR4-P21-n252: 3 premaxilares, 1 maxilar izquierdo, 1 maxilar derecho, 2 orbitoesfenoides izquierdos, 2 orbitoesfenoides derechos, 1 frontal izquierdo, 1 frontal derecho, 4 vomero-palatinos derechos, 8 paraesfenoides, 4 húmeros izquierdos, 4 húmeros derechos, 1 tibia izquierda, 1 ilion izquierdo, 1 ilion derecho, 60 vértebras dorsales, 14 vértebras caudales.

— MIR4-Q20-n261: 1 premaxilar, 1 maxilar derecho, 2 dentarios derechos, 1 frontal izquierdo, 3 atlas, 73 vértebras dorsales, 19 vértebras caudales, 2 escápula-coracoides izquierdo, 1 escápula-coracoides derecho, 4 húmeros izquierdos, 5 húmeros derechos, 3 fémures izquierdos, 5 fémures derechos.

— MIR4-Q20-n262: 4 dentarios izquierdos, 3 dentarios derechos, 5 premaxilares, 3 maxilares izquierdos, 2 maxilares derechos, 1 vomerio izquierdo, 1 orbitoesfenoides izquierdo, 6 paraesfenoides, 3 frontales izquierdos, 3 escápula-coracoides derechos, 6 húmeros izquierdos, 8 húmeros derechos, 2 iliones derechos, 13 fémures izquierdos, 8 fémures derechos, 1 tibia izquierda, 1 tibia derecha, 3 atlas, 72 vértebras dorsales, 40 vértebras caudales.

— MIR4-P21-n267: 1 vértebra caudal.

— MIR5-P22-n1: 1 vértebra dorsal, 1 vértebra caudal.

— MIR5-P22-n2: 1 atlas, 7 vértebras dorsales, 1 húmero izquierdo.

— MIR5-P21-n7: 1 húmero izquierdo.

Diagnosis: los paraesfenoides adscritos a *L. helveticus* presentan el característico contorno sub-hexagonal de ángulos marcados en la porción posterior, con seis pequeños lóbulos proyectados posterolateralmente en vista dorsal (Gleed-Owen, 1998) (Figura 4.3.A).

Los frontales en *Lissotriton* tienen una forma sub-triangular y en *L. helveticus* la proyección posterolateral del frontal es larga y conecta con el hueso escamoso formando un arco óseo continuo, a diferencia de *Lissotriton vulgaris* que es discontinuo debido al corto desarrollo de la proyección posterolateral (Gleed-Owen, 1998).

Las vértebras dorsales del género *Lissotriton*, siempre de tamaño pequeño (longitud del centrum vertebral menor de 3 mm), en vista lateral exhiben crestas dorsales laterales que terminan en su extremo posterior entre las apófisis transversales dorsales y ventrales (Buckley y Sanchiz, 2012) (Figura 4.3.C.3). Las vértebras dorsales de la muestra se adscriben a *L. helveticus* por la forma en "U" de la muesca posterior de la cresta neural en vista dorsal (Figura 4.3.C.1, en contraste con la muesca en forma de "W" propia de *Lissotriton vulgaris* (Holmann y Stuart, 1991).

Las vértebras caudales del género *Lissotriton* tienen las apófisis neural y hemal estrechas y alargadas, a diferencia de otros salamándridos que las tienes menos desarrolladas (Figura 4.3.D.1-3). En *L. helveticus*, las terminaciones de ambas apófisis son muy agudas, con un perfil angular muy marcado en vista anterior (Figura 4.3.D.1), mientras que en *L. vulgaris* acaban en formas redondeadas o cuadradas (Gleed-Owen, 1998). En vista anterior, las vértebras caudales no exhiben un constreñimiento lateral del arco hemal (Figura 4.3.D.1), a diferencia de *T. marmoratus* (Gleed-Owen, 1998), el otro salamándrido de la muestra.

Los húmeros de la muestra adscritos a *Lissotriton* son todos de pequeño tamaño y no tienen fosa del olocraneon o ésta aparece muy poco desarrollada en vista dorsal (Ratnikov, 2015).

Género *Triturus* Rafinesque, 1815

Triturus marmoratus (Latreille, 1800)

Figuras 3.4.A, 4.3.E-G

Material examinado:

— MIR4-P21-n252: 1 maxilar izquierdo, 1 maxilar derecho, 1 vomero-palatino derecho, 1 orbitoesfenoides izquierdo, 2 paraesfenoides, 1 húmero izquierdo, 1 húmero derecho, 7 vértebras dorsales, 5 vértebras caudales.

— MIR4-Q20-n261: 1 premaxilar fragmentario, 2 dentarios izquierdos, 2 dentarios derechos, 1 vomerio izquierdo, 1 frontal izquierdo, 1 frontal derecho, 1 paraesfenoides, 1 orbitoesfenoides derecho, 1 escápula-coracoides derecho, 3 húmeros izquierdos, 1 húmero derecho, 2 fémures izquierdos, 1 fémur derecho, 1 atlas, 26 vértebras dorsales, 2 vértebra caudal, 2 costillas.

— MIR4-Q20-n262: 2 dentarios izquierdos, 2 dentarios derechos, 1 premaxilar, 1 maxilar derecho, 2 paraesfenoides, 2 frontales izquierdos, 1 frontal derecho, 1 fémur izquierdo, 1 fémur derecho, 1 atlas, 14 vértebras dorsales, 4 vértebras caudales, 4 costillas.

— MIR4-P21-n267: 1 vértebra dorsal, 5 vértebras dorsales fragmentarias.

— MIR5-P22-n1: 1 húmero derecho, 2 vértebras dorsales fragmentarias.

— MIR5-P22-n2: 1 orbitoesfenoides derecho, 1 vértebra dorsal, 1 fémur izquierdo fragmentario.

— MIR5-P21-n4: 1 premaxilar, 1 maxilar izquierdo, 2 maxilares derechos, 1 dentario izquierdo, 1 paraesfenoides, 1 radio, 1 atlas, 20 vértebras dorsales, 2 vértebras caudales, 2 fémures derechos, 1 húmero izquierdo, 1 húmero derecho, 1 costilla anterior, 1 costilla posterior.

Diagnosis: el premaxilar en el género *Triturus* es un hueso par de gran tamaño, con ambas partes fusionadas medialmente. Sus las proyecciones posteriores son paralelas y también parcialmente fusionadas (Gleed-Owen, 1998). Un premaxilar en MIR5-P21-n4 aparece fusionado, por lo que se adscribe al grupo de *Triturus* sensu lato, y su tamaño grande lo acerca a *T. marmoratus*. No obstante, este premaxilar tiene proyecciones posteriores divergentes y sin fusionar, a diferencia de lo más frecuente en esta especie.

Los paraesfenoides presentan un ligero estrechamiento de la región posterior que se hace más pronunciado una vez ultrapasado la mitad de su longitud, coincidente con lo descrito en *T. marmoratus*, con contornos más redondeados sin el perfil sub-hexagonal de *L. helveticus* (Gleed-Owen, 1998) (Figura 4.3.E).

Los frontales de *T. marmoratus* tienen forma sub-rectangular y las proyecciones posterolaterales conectan con el hueso parietal, lo que genera un ensanchamiento de la región posterior del frontal (Gleed-Owen, 1998).

Las vértebras dorsales de *T. marmoratus* son de gran tamaño, relativamente largas comparadas con otros salamándridos, y se caracterizan por la presencia de una cresta neural larga que termina en una muesca formada por una bifurcación posterior,

generando en vista dorsal una forma de "V" sobre la zona distal vertebral (Gleed-Owen, 1998) (Figura 3.4.A.1). En la muestra aparentemente hay vértebras dorsales de como mínimo tres tamaños diferentes: un primer grupo perteneciente a individuos de gran tamaño, con vértebras dorsales de 4.8 – 5.4 mm de media de longitud, un segundo grupo con vértebras dorsales de 3.9 – 4.3 mm y, finalmente, un tercer formado por juveniles e inmaduro, con vértebras dorsales de 2.1 – 2.4 mm. Así mismo, la cresta dorsal lateral llega a la apófisis transversal dorsal en vista lateral, a diferencia de *Lissotriton* (Buckley y Sanchiz, 2012) (Figura 3.4.A.3).

Las vértebras caudales de *T. marmoratus* son muy parecidas a las de *L. helveticus*, si bien alcanzan mayores dimensiones. El principal elemento diagnóstico es el constreñimiento lateral del arco hemal en vista anterior, a modo de "ojo de cerradura", presente tanto en individuos juveniles como en adultos, y que permite diferenciar a los *T. marmoratus* inmaduros de *L. helveticus* (Gleed-Owen, 1998).

Los húmeros de la muestra adscritos a *Triturus* tienen fosa del olocraneon bien desarrollada y distinguible en vista dorsal, a diferencia de *Lissotriton* (Ratnikov, 2015).

Orden ANURA Fischer von Waldheim, 1813

Familia Alytidae Fitzinger, 1843

Género *Alytes* Wagler, 1829

Alytes obstetricans (Laurenti, 1768)

Figura 4.3.H

Material examinado:

— MIR5-P22-n2: 1 húmero derecho, 1 ilion derecho fragmentario, 1 fémur.

— MIR5-P21-n7: 1 ilion izquierdo, 1 ilion derecho.

***Diagnosis*:** el húmero de *Alytes obstetricans* tiene la diáfisis curvada, moderadamente robusta y con el cóndilo desplazado lateralmente (Bailon, 1999; Blain, 2009). Presenta cresta paraventral y se caracteriza por la presencia de una fosa cubital cerrada por el lado radial y por el desarrollo robusto de los epicóndilos ulnar y radial (Bailon, 1999).

El ilion en *Alytes* no tiene cresta dorsal en la proyección anterior pero sí presenta el tubérculo superior (Bailon 1999), que se sitúa mayormente sobre la cavidad acetabular (Blain, 2009) (Figura 4.3.H). Otro elementos elementos diagnósticos del ilion son el proceso isquiónico (= *pars ascendens*) largo y la presencia de surco y tubérculo interilíacos en vista distal (Bailon, 1999).

El fémur tiene la cresta femoral poco desarrollada (Bailon, 1999).

Familia Pelobatidae Bonaparte, 1850

Género *Pelobates* Wagler, 1830

Pelobates cultripes (Cuvier, 1829)

Figura 4.3.K

Material examinado:

— MIR4-Q21-n233: 1 escamoso derecho, 1 angular izquierdo, 1 supraescápula izquierda.

— MIR4-Q21-n235: 1 maxilar izquierdo, 1 frontoparietal fragmentario.

— MIR5-P22-n2: 1 angular izquierdo, 1 coracoides derecho, 1 ilion izquierdo fragmentario, 1 radioulna fragmentaria.

— MIR5-P21-n7: 1 húmero izquierdo, 1 húmero derecho, 1 coracoides derecho, 2 iliones izquierdos, 1 ilion derecho, 1 tibiofíbula fragmentario, 2 fémures fragmentarios, 2 vértebras dorsales, 1 vértebra sacra.

***Diagnosis*:** ambos frontoparietales están completamente fusionados en *Pelobates*, a diferencia del resto de anuros ibéricos, y presentan en su superficie dorsal una gran ornamentación dérmica. El proceso escamosal de los frontoparietales está bien desarrollado en *Pelobates cultripes*, a diferencia de *Pelobates fuscus* (Bailon, 1999).

El hueso escamoso de *P. cultripes* tiene el proceso frontoparietal ancho y también una abundante ornamentación dérmica (Bailon, 1999), también ausente en el resto de los anuros presentes en la Península Ibérica.

Los húmeros de la muestra tienen la diáfisis curvada, cresta paraventral y cóndilo desplazado hacia el exterior, caracteres que comparten con *Alytes*, pero a diferencia de este género tienen la fosa cubital abierta por el lado radial (Bailon, 1999).

Las vértebras dorsales, procélicas con el acetábulo y el cóndilo circulares, tienen un arco neural largo y la cresta neural se prolonga en una punta posterior muy desarrollada que sobrepasa las postzigapófisis (Bailon, 1999, Blain, 2009).

La vértebra sacra, con un acetábulo anterior y un cóndilo posterior que no está soldado con el uróstilo, tiene un gran desarrollo de las apófisis laterales en sentido antero-posterior (Bailon, 1999).

El ilion de *Pelobates* no tiene cresta dorsal y tampoco presenta tubérculo superior, y se caracteriza por la presencia de estriaciones de su superficie postero-medial (Bailon, 1999) (Figura 4.3.K).

Familia Hylidae Rafinesque, 1814

Género *Hyla* Laurenti, 1768

Hyla molleri (Bedriaga, 1889)

(*Hyla* gr. *Hyla arborea*)

Figura 3.5.A-T, 4.3.I-J

Material examinado:

— MIR4-Q21-n227: 2 angulares izquierdos, 1 fémur.

— MIR4-Q21-n234: 1 ilion derecho.

— MIR4-Q21-n245: 1 ilion derecho, 1 isquion-pubis, 1 vértebra dorsal, 1 falange.

— MIR4-P21-n246: 1 vértebra sacra.

— MIR4-P21-n252: 1 húmero izquierda (macho), 1 húmero derecho (macho), 1 vértebra dorsal, 1 vértebra sacra, 1 tibiofíbula, 1 ilion izquierdo.

— MIR4-Q20-n261: 1 escápula izquierda, 1 escápula derecha, 1 húmero izquierdo (macho), 1 húmero derecho (macho), 2 húmeros fragmentarios, 2 radioulnas izquierdas, 5 vértebra dorsales, 3 vértebras sacras, 2 uróstilos, 3 iliones derechos.

— MIR4-Q20-n262: 1 premaxilar izquierdo, 1 escamoso izquierdo, 1 pterigoides derecho, 1 paraesfenoides, 1 proótico-exoccipital izquierdo, 1 proótico-exoccipital derecho, 1 supraescápula izquierda, 1 escápula izquierda, 1 escápula derecha, 2 clavículas izquierdas, 1 clavícula derecha, 1 coracoides izquierdo, 1 coracoides derecho, 1 húmero izquierdo (macho), 1 húmero derecho (macho), 1 fémur, 2 tibiofíbulas, 1 falange, 2 atlas, 5 vértebras dorsales, 1 vértebra sacra, 1 uróstilo.

— MIR4-P21-n267: 1 ilion izquierdo, 1 isquion-pubis, 1 radioulna derecha, 3 tibiofíbulas fragmentarias, 1 vértebra dorsal, 1 escápula izquierda, 1 húmero izquierdo (macho).

— MIR4-P22-n380: 1 tibiofíbula.

— MIR5-P22-n1: 1 maxilar fragmentario, 2 angulares izquierdos, 1 angular derecho, 1 clavícula izquierda, 1 atlas, 1 vértebra sacra, 2 uróstilos, 1 ilion derecho, 1 fémur.

— MIR5-P22-n2: 1 premaxilar izquierdo, 5 maxilares izquierdos, 6 maxilares derechos, 6 pterigoides izquierdos, 4 pterigoides derechos, 2 escamosos izquierdos, 3 escamosos derechos, 7 esfenetmoides, 21 proótico-exoccipitales izquierdos, 15 proótico-exoccipitales derechos, 24 proótico exoccipitales fragmentarios, 10 angulares izquierdos, 6 angulares derechos, 12 paraesfenoides, 2 supraescápulas izquierdas, 3 supraescápulas derechas, 24 escápulas izquierdas, 30 escápulas derechas, 6 clavículas izquierdas, 7 clavículas derechas, 19 coracoides izquierdos, 23 coracoides derechos, 16 húmeros izquierdos (10 machos, 5 hembras y 1 indeterminado), 22 húmeros derechos (11 machos, 6 hembras y 5 indeterminados), 19 radioulnas izquierdas, 20 húmeros fragmentarios, 21 radioulnas derechas, 12 atlas, 168 vértebras dorsales, 33 vértebras sacras, 33 iliones izquierdos, 32 iliones derechos, 18 isquion-pubis, 40 fémures, 44 tibiofíbulas, 57 tarsos.

— MIR5-P21-n4: 6 premaxilares izquierdos, 7 premaxilares derechos, 27 maxilares izquierdos, 21 maxilares derechos, 12 angulares izquierdos, 6 angulares derechos, 12 pterigoides, 19 paraesfenoides, 25 esfenetmoides, 48 proótico-exoccipitales izquierdos, 44 proótico-exoccipitales derechos, 39 atlas, 389 vértebras dorsales, 57 vértebras sacras, 59 iliones izquierdos, 66 iliones derechos, 20 isquiones, 53 uróstilos, 58 húmeros izquierdos, 50 húmeros derechos, 6 húmeros fragmentarios, 58 escápulas izquierdas, 49 escápulas derechas, 38 coracoides, 8 clavículas, 93 radio-ulnas, 120 fémures, 131 tibiofíbulas,187 tarsos.

— MIR5-P21-n7: 1 atlas, 1 ilion derecho, 3 vértebras dorsales, 2 tibiofíbulas, 1 coracoides derecho, clavícula izquierda, 1 húmero izquierdo (macho), 1 húmero derecho (macho).

— MIR5-P22-n13: 1 maxilar derecho, 5 pterigoides izquierdos, 2 pterigoides derechos, 9 paraesfenoides, 2 esfenetmoides, 6 angulares izquierdos, 8 angulares derechos, 1 supraescápula izquierda, 4 supraescápulas derechas, 8 escápulas izquierdas, 9 escápulas derechas, 4 coracoides izquierdos, 12 coracoides derechos, 1 clavícula izquierda, 2

clavículas derechas, 2 húmeros izquierdos (1 macho, 1 hembra), 12 húmeros derechos (8 machos, 1 hembra, 3 indeterminados), 4 húmeros fragmentarios, 6 radioulnas izquierdas, 8 radioulnas derechas, 2 radioulnas fragmentarias, 5 atlas, 61 vértebras dorsales, 11 vértebras sacras, 10 uróstilos, 21 iliones izquierdos, 13 iliones izquierdos, 3 isquion-pubis, 38 fémures, 36 tibiofíbulas.

***Diagnosis*:** los restos adscritos a *Hyla* gr. *H. arborea* destacan por su reducido tamaño y fragilidad en comparación con otros anuros ibéricos. El principal elemento óseo utilizado para la determinación taxonómica del género *Hyla* es el ilion, caracterizado por la presencia de un tubérculo superior de forma globular en vista lateral, por la presencia de un proceso púbico (= *pars descendens*) con una proyección alargada ventralmente y por la ausencia de un cresta dorsal (Bailon, 1999) (Figura 3.5.T).

Otro elemento diagnóstico para *Hyla* es la escápula, de morfología destacadamente alargada y delgada en comparación con el resto de anuros ibéricos, en la que destaca la gran separación existente entre los procesos glenoideo y acrominal en vistas dorsal y ventral (Bailon, 1999; Blain, 2009) (Figura 3.5.M).

El húmero de *Hyla* se caracteriza por una diáfisis recta y delicada en vista ventral sin presencia de una cresta paraventral; el cóndilo aparece desplazado lateralmente respecto al eje de la diáfisis, formando en vista ventral una fosa cubital, con la presencia de una cresta radial, así como de epicóndilos ulnar y radial bien desarrollados en el extremo distal del ilion (Bailon, 1999) (Figura 3.5.N).

La asignación al clado *Hyla* gr. *H. arborea* se asienta en la morfología del tubérculo superior del ilion. Las especies del grupo *arborea*, representado en la Península Ibérica por *Hyla molleri*, presentan un tubérculo superior bajo y generalmente ovalado en su base, sin una forma triangular de su porción elevada (Figura 3.5.T), mientras que en *Hyla meridionalis* sí presenta una porción triangular elevada y con una terminación redondeada en su ápice (Holman, 1992, 1998).

Familia Bufonidae Laurenti, 1768

Género *Bufo* Laurenti, 1768

Bufo spinosus Daudin, 1803

(*Bufo* gr. *Bufo bufo*)

Figura 4.3.P-Q

Material examinado:

— MIR4-Q20-n261: 1 escápula izquierda.

— MIR5-P21-n7: 1 atlas, 10 vértebras dorsales, 6 vértebras dorsales fragmentarias, 2 vértebras sacras, 2 uróstilos, 1 escápula izquierda, 2 escápula derecha, 1 radioulna izquierda, 2 radioulna derecha, 1 ilion izquierdo, 1 ilion derecho.

— MIR5-P22-n13: 1 escápula izquierda.

***Diagnosis*:** el atlas de *Bufo* gr. *B. bufo*, procélico con el cóndilo posterior aplanado dorsol-ventralmente, tiene un arco neural corto y la punta posterior poco diferenciada. El centrum vertebral del atlas es robusto y está bien individualizado, también las paredes laterales que

forman un arco neural ojival, característico de *Bufo* gr. *B. bufo* (Bailon, 1999).

Las vértebra dorsales en los bufónidos también son procélicas, con el arco neural corto y las apófisis transversas generalmente dirigidas transversalmente, y se caracterizan por el centrum vertebral desarrollado y las paredes laterales robustas y cortas (Bailon, 1999).

La vértebra sacra en Bufonidae tiene acetábulo anterior, cresta neural y apófisis sacras extendidas antero-posteriormente pero con menor desarrollo en comparación con *Pelobates* y *Pelodytes*. En *Bufo* gr. *B. bufo* la base de las apófisis sacras carece de fosetas visibles en vista dorsal (Bailon, 1999).

Bufonidae presenta escápulas robustas, más altas que anchas y con la apófisis glenoide separada del cuerpo óseo (Figura 4.3.Q). Las escápulas de *Bufo* gr. *B. bufo* carecen de fosa glenoide (Figura 4.3.Q.1), lo que permite diferenciarlas del otro bufónido ibérico, *Epidalea calamita* (Bailon, 1999). Una escápula izquierda proveniente de MIR5-P22-n13 tiene una cresta anterior desarrollada (Figura 4.3.Q).

En *Bufo* gr. *B. bufo* el ilion no tiene cresta dorsal, el proceso isquiónico es corto y la tubérculo superior del ilion tiene forma unilobulada, terminada en un borde dorsal redondeado (Bailon, 1999) (Figura 4.3.P).

En la Península Ibérica el clado *Bufo* gr. *B. bufo* está representado únicamente por la especie *Bufo spinosus*, que abarca también el Magreb y el sur, oeste y centro de Francia (Arntzen et al., 2013).

Género *Epidalea* Cope, 1864

Epidalea calamita (Laurenti, 1768)

Figura 4.3.N-O

Material examinado:

— MIR4-Q21-n228: 1 escápula derecha.

— MIR4-Q21-n231: 1 húmero izquierdo.

— MIR4-Q21-n233: 6 vértebras dorsales (incluyendo 1 vértebra dorsal segunda), 1 húmero izquierdo, 1 ilion izquierdo, 2 fémures, 2 tibiofíbulas izquierdas, 1 tarso.

— MIR4-P21-n243: 6 vértebras dorsales fragmentarias, 1 supraescápula derecha, 1 escápula izquierda, 1 ilion derecho, 1 isquion-pubis, 1 tibiofíbula fragmentaria, 1 radioulna fragmentaria, 9 falanges.

— MIR5-P22-n1: 1 angular derecho, 1 vértebra dorsal, 1 ilion derecho, 2 falanges.

Diagnosis: la escápula de *Epidalea calamita* tiene una configuración muy parecida a la de *Bufo* gr. *B.* bufo, pero difiere por la presencia de una fosa supraglenoide sobre la apófisis glenoide (Bailon, 1999) (Figura 4.3.O).

Los húmeros de la muestra adscritos a *E. calamita* son robustos y moderadamente cortos, con la diáfisis curvada y el cóndilo desplazado hacia el exterior. La fosa cubital aparece cerrada y tanto el epicóndilo como los epicóndilos ulnar y radial están bien desarrollados (Bailon, 1999).

El ilion también es parecido al de *Bufo* gr. *B. bufo*, pero presenta dos importantes diferencias en *E. calamita*: el tubérculo superior tiene una forma puntiaguda en vista lateral y sobre la

proyección anterior hay desarrollada una excrecencia posterio-ventral a modo de lámina alargada ("*lame calamite*") (Bailon, 1999; Blain, 2009) (Figura 4.3.N).

Familia Ranidae Rafinesque, 1814

Género *Rana* Linnaeus, 1758

Rana temporaria Linnaeus, 1758

Figuras 3.4.B-C, 4.3.L-M

Material examinado:

— MIR4-Q21-n235: 1 vértebra dorsal.

— MIR4-Q20-n261: 1 angular izquierdo, 2 angulares derechos, 1 frontoparietal derecho, 4 paraesfenoides, 5 iliones izquierdos, 4 iliones derechos, 5 coracoides izquierdos, 2 coracoides derechos, 3 escápulas izquierdas, 1 escápula derecha, 2 húmeros izquierdos (machos), 3 húmeros derechos (machos), 4 húmeros fragmentarios, 1 radioulna izquierda, 2 radioulnas derechas, 1 fémur, 4 tibiofíbulas fragmentarias, 8 vértebras dorsales fragmentarias (incluyendo 1 vértebra dorsal 8ª), 2 vértebras sacras.

— MIR4-Q20-n262: 1 premaxilar izquierdo, 1 angular izquierdo, 1 angular derecho, 2 paraesfenoides, 1 frontoparietal izquierdo, 3 frontoparietales derechos, 1 pterigoides izquierdo, 1 escápula izquierda, 3 escápulas derechas, 1 coracoides izquierdo, 1 húmero izquierdo (macho), 1 húmero izquierdo (hembra), 3 húmeros derechos fragmentarios, 3 húmeros derechos fragmentarios, 1 radioulna izquierda, 1 radioulna derecha, 1 radioulna fragmentaria, 2 fémures, 6 iliones izquierdos, 12 vértebras dorsales (incluyendo 3 vértebras dorsales 8ªs), 3 vértebras sacras, 6 iliones derechos, 2 isquiones-pubis.

— MIR5-P22-n2: 1 escamoso izquierdo, 1 frontoparietal izquierdo, 1 frontoparietal derecho, 2 angulares izquierdos, 1 angular derecho, 1 paraesfenoides, 1 escápula izquierda, 2 escápulas derechas, 1 coracoides izquierdo, 2 coracoides derechos, 1 húmero izquierdo (macho) 2 atlas, 5 vértebras dorsales (incluyendo 2 vértebras 8ª), 2 vértebras sacras, 1 uróstilo, 1 ilion derecho fragmentario, 1 isquion-pubis, 2 tibiofíbulas fragmentarias.

— MIR5-P21-n4: 1 premaxilar izquierdo, 1 premaxilar derecho, 1 maxilar izquierdo, 1 maxilar derecho, 1 angular izquierdo, 1 angular derecho, 1 vomerio derecho, 1 paraesfenoides, 1 frontoparietal derecho, 5 vértebras dorsales, 1 ilion derecho, 1 clavícula izquierda, 1 clavícula derecha, 1 radio-ulna izquierda, 1 radio-ulna derecha, 1 húmero izquierdo, 1 húmero derecho, 1 escápula derecha, 1 escápula izquierda, 1 coracoides, 1 tibiofíbula, 1 tarso.

***Diagnosis*:** el frontoparietal presenta una cresta occipital marcada y una cresta medial recta, caracteres diagnósticos que se adscriben a *Rana temporaria* (Bailon, 1999; Blain y Arribas, 2017).

Las escápulas preservadas son más largas que anchas y presentan el proceso glenoideo parcialmente cubierto por el proceso acromial en vista ventral (Figura 3.4.C.1), así como se observa también en vista ventral la formación de una cresta interna que discurre sobre el proceso

acromial y lámina ósea, caracteres diagnósticos que las asignan al género *Rana* (sensu estricto) (Bailon, 1999) (Figura 3.4.C.1). La escasa distancia en la constricción medial de la escápula entre la cresta interna y el margen anterior del hueso en vista ventral se asocia a las especies *R. temporaria* y *Rana dalmatina* (Blain, 2005, 2009; Blain y Arribas, 2017) (Figura 3.4.C.2).

El coracoides presenta una concavidad acusada de su margen anterior, lo que se adscribe a *R. temporaria* y a *Rana iberica*, y su constricción medial es relativamente robusta, carácter propio de *R. temporaria* en contraste con la constricción medial más esbelta del coracoides, carácter asociado al resto de especies ibéricas del género *Rana* (Blain y Arribas, 2017).

Los húmeros presentan la diáfisis fina y recta en vista ventral, así como el cóndilo situado dentro del eje marcado por la diáfisis (Figura 3.4.B). La cresta medial de los individuos masculinos se curva dorsalmente y continúan su desarrollo hasta el tercio inferior de la diáfisis, como corresponde en las especies del género *Rana* (Bailon, 1999) (Figura 3.4.B).

Los iliones de *R. temporaria*, que tienen un proceso isquiónico corto y no presentan tubérculo ni surco inter-ilíacos, destacan por la presencia de una cresta dorsal de gran desarrollo por la proyección anterior pero relativamente baja, que se curva medialmente y se prolonga hasta el tuber posterior, donde la cresta dorsal alcanza su punto más alto (Bailon, 1999; Blain y Arribas, 2017).

Orden SQUAMATA Oppel, 1811

Familia Anguidae Oppel, 1811

Género *Anguis* Linnaeus, 1758

Anguis fragilis Linnaeus, 1758

Figuras 3.4.D, 4.3.R

Material examinado:

— MIR4-Q21-n228: 1 dentario derecho, 1 maxilar izquierdo, 20 vértebras dorsales, 1 vértebra sacra.

— MIR4-Q21-n231: 1 maxilar fragmentario derecho.

— MIR4-Q21-n234: 1 dentario derecho, 8 vértebras dorsales.

— MIR4-P21-n243: 1 maxilar izquierdo, 1 maxilar derecho, 1 dentario izquierdo, 1 dentario derecho, 1 frontal izquierdo, 1 parietal, 50 vértebras dorsales, 12 vértebras caudales anteriores, 5 vértebras caudales posteriores.

— MIR4-P21-n252: 1 dentario izquierdo.

— MIR4-P22-n380: 1 dentario izquierdo, 9 vértebras caudales anteriores, 12 vértebras caudales posteriores.

— MIR5-P22-n1: 11 vértebras dorsales, 2 vértebras caudales anteriores, 4 vértebras caudales posteriores.

— MIR5-P22-n2: 1 vértebra dorsal, 1 vértebra dorsal fragmentaria, 1 vértebra caudal fragmentaria.

— MIR5-P21-n4: 3 vértebras dorsales, 2 vértebras caudales completas (sin arco hemal), 6 partes proximales de vértebras caudales, 1 parte distal de vértebra caudal, 1 arco hemal.

— MIR5-P21-n7: 17 vértebras dorsales, 5 vértebras caudales.

Diagnosis: los dientes en maxilares y dentarios de *Anguis fragilis* son elementos muy diagnósticos, con una morfología caniniforme que comparten con otros miembros de la tribu Anguini dentro de la subfamilia Anguinae (Augé, 2005).

Las vértebras dorsales de *A. fragilis* también son muy distintivas respecto al resto de integrantes de Squamata de la Península Ibérica por su morfología especial: presentan la característica forma procoela de pequeño tamaño (longitud del centrum vertebral menor de 3 mm), con el centrum vertebral más largo que ancho y con la superficie ventral aplanada en vistas ventral (Figura 3.4.D.2) y lateral (Figura 3.4.D.4), y con el cóndilo y el cótilo aplanados dorso-ventralmente en vista anterior (Figura 3.4.D.3) (Blain, 2009). Las superficies articulares de las prezigapófisis (en vista dorsal, Figura 3.4.D.1) y de las postzigapófisis (en vista ventral, Figura 3.4.D.2) presentan formas ovaladas con una inclinación hacia arriba y dirigidas moderadamente hacia delante (Blain, 2009). En las vértebras dorsales la neuroespina, larga y moderadamente alta, termina en una punta que no supera en vista dorsal el límite posterior de las postzigapófisis en vista dorsal (Figura 3.4.D.1) (Blain, 2009).

Las vértebras caudales presentan una neuroespina muy desarrollada y con una proyección dorso-posterior marcada, que en vista lateral se extiende hasta el límite de las postzigapófisis; así como en vista dorsal y ventral presenta un par de procesos transversales que partes desde el centrum vertebral, que en vista anterior presentan una leve inclinación hacia abajo (Gleed-Owen, 1998)

Familia Scincidae Oppel, 1811

Género *Chalcides* Laurenti, 1768

Chalcides striatus (Cuvier, 1829)

Figuras 3.4.E-F, 4.3.S-T

Material examinado:

— MIR4-Q21-n227: 5 maxilares izquierdos, 1 maxilar derecho, 4 dentarios izquierdos, 2 dentarios derechos, 1 cuadrado izquierdo, 1 cuadrado derecho, 1 vomerio izquierdo, 2 frontales izquierdos, 2 frontales derechos, 1 esfenoides, 28 vértebras dorsales, 2 vértebras sacras, 10 vértebras caudales anteriores, 13 vértebras caudales posteriores.

— MIR4-Q21-n228: 3 maxilares izquierdos, 2 maxilares derechos, 5 dentarios izquierdos, 1 dentario derecho, 4 parietales, 1 cuadrado izquierdo, 1 cuadrado derecho, 5 frontales izquierdos, 4 frontales derechos, 3 coronoides izquierdos, 2 coronoides derechos, 3 esfenoides 5 vomerios izquierdos, 6 vomerios derechos, 1 articular izquierdo, 3 articulares derechos, 82 vértebras dorsales, 2 vértebras sacras, 4 vértebras caudales anteriores, 35 vértebras caudales posteriores.

— MIR4-Q21-n231: 12 dentarios izquierdos, 12 dentarios derechos, 3 maxilares izquierdos, 8 maxilares derechos, 5 vomerios izquierdos, 6 vomerios derechos, 4 parietales, 5 frontales izquierdo, 7 frontales derechos, 1 articular izquierdo, 2 articular derecho, 3 surangulares izquierdos, 2 surangulares derechos, 4 esfenoides, 3 cuadrados izquierdos, 4 cuadrados derechos, 181 vértebras dorsales, 2 vértebra sacras, 79

vértebras caudales anteriores, 42 vértebras caudales posteriores

— MIR4-Q21-n233: 1 dentario izquierdo, 1 dentario derecho, 1 esfenoides, 4 vértebras dorsales, 3 vértebras caudales posteriores, 3 costillas.

— MIR4-Q21-n234: 1 dentario izquierdo, 1 vomerio izquierdo, 1 coronoides izquierdo, 2 coronoides derechos, 16 vértebras dorsales, 4 vértebras dorsales anteriores, 12 vértebras caudales posteriores.

— MIR4-Q21-n235: 7 dentarios izquierdos, 6 dentarios derechos, 1 cuadrado izquierdo, 4 cuadrados derechos, 5 maxilares izquierdos, 5 maxilares derechos, 3 vomerios izquierdos, 5 vomerios derechos, 3 escápulas izquierdas, 1 escápula derecha, 7 parietales, 3 frontales derechos, 3 frontales izquierdos, 2 esfenoides, 1 coronoides izquierdo, 3 articulares izquierdos, 3 articulares derechos, 206 vértebras dorsales, 10 vértebras sacras, 97 vértebras caudales anteriores, 80 vértebras caudales posteriores.

— MIR4-Q21-n245: 1 dentario derecho fragmentario, 2 parietales, 27 vértebras dorsales, 5 vértebras caudales anteriores, 10 vértebras caudales posteriores.

— MIR4-P21-n252: 1 dentario izquierdo, 1 vértebra caudal anterior, 3 vértebras caudales posteriores.

— MIR4-Q20-n262: 1 dentario derecho, 1 coronoides derecho, 1 vomerio izquierdo.

— MIR5-P21-n4: 1 dentario izquierdo, 1 dentario derecho.

— MIR4-P21-n267: 1 vértebra dorsal, 4 vértebras dorsales fragmentarias, 5 vértebras caudales anteriores fragmentarias.

— MIR4-P22-n380: 1 dentario izquierdo, 1 cuadrado izquierdo, 1 cuadrado derecho, 8 vértebras dorsales.

— MIR5-P22-n1: 1 vértebra dorsal anterior, 9 vértebras dorsales, 1 vértebra sacra, 2 vértebras caudales anteriores.

— MIR5-P22-n2: 1 maxilar izquierdo, 1 dentario izquierdo, 1 vomerio izquierdo, 1 frontal derecho, 3 vértebras dorsales, 7 vértebras caudales.

— MIR5-P21-n4: 1 dentario izquierdo, 1 dentario derecho.

***Diagnosis*:** en los maxilares y dentarios examinados aparecen dientes pleurodontes, isodontes, cilíndricos, monocúspides y con ápices de terminación roma, caracteres diagnósticos en la dentición del género *Chalcides* y que lo diferencian de los lacértidos (Bailon, 1991; Blain, 2009 (Figura 3.4.E-F)). También es propio de *Chalcides*, así como del resto de Scincoidea, la presencia de un proceso coronoide lateral alargado en el dentario, que se extiende dorsalmente hasta alcanzar la superficie anterolateral del coronoides (Estes et al., 1988). En vista labial, el proceso coronoides lateral no tiene una impresión articular, a diferencia de los lacértidos (Blain, 2009) (Figura 3.4.F). El conteo de posiciones dentales de los dentarios varía entre los 19 y 20 dientes (Figura 3.4.F), lo que lo sitúa dentro del número de posiciones dentales para *Chalcides striatus* (36-42) y

fuera de la otra especie ibérica, *Chalcides bedriagai* (31-36) (Caputo, 2004).

Las vértebras dorsales de *Chalcides* son procélicas, alargadas y en vista dorsal presentan un ligero estrechamiento interzigapofisario, mientras que en vista anterior presentan el arco neural moderadamente deprimido (Blain, 2009). Tanto el cóndilo como el cótilo aparecen ligeramente aplanados dorso-ventralmente (Blain, 2009). En las vértebras dorsales, la neuroespina es baja, delgada y larga, y se proyecta posteriormente formando una punta que se finaliza más allá del límite posterior de las postzigapófisis en vista dorsal, a diferencia de otros escamosos como *A. fragilis* (Blain, 2009).

Las vértebras caudales anteriores son comparativamente más cortas y presentan una constricción interzigapofisario más acentuada en comparación con las vértebras dorsales (Blain, 2009).

Familia Lacertidae Oppel, 1811

Género *Lacerta* Linnaeus, 1758

Lacerta cf. *bilineata* (Daudin, 1802)

Figuras 3.4.H-J, 4.3.V-X

Material examinado:

— MIR4-P21-n243: 1 dentario derecho, 1 frontal izquierdo, 18 vértebras dorsales, 1 vértebra sacra.

— MIR4-P21-n252: 1 frontal izquierdo, 1 vértebra dorsal fragmentaria.

— MIR5-P22-n1: 1 axis, 1 cuadrado derecho, 1 vértebra dorsal fragmentaria.

— MIR5-P22-n2: 1 dentario izquierdo fragmentario, 1 cuadrado derecho.

— MIR5-P21-n4: 2 maxilares izquierdos, 3 maxilares derechos, 3 cuadrados izquierdos, 2 cuadrados derechos, 1 frontal derecho, 2 parietales, 1 yugal izquierdo, 1 yugal derecho, 1 esfenoides, 1 dentario izquierdo, 1 dentario derecho, 1 esplenial izquierdo, 1 articular izquierdo, 1 articular derecho, 6 vértebras cervicales, 21 vértebras dorsales, 2 vértebras sacras, 9 vértebras post-sacrales, 4 partes proximales de vértebras caudales, 7 partes distales de vértebras caudales, 14 costillas, 1 escápula-coracoides izquierdo, 1 húmero izquierdo, 1 radio izquierdo, 1 radio derecho, 1 tarso, 1 ilion derecho, 1 isquion izquierdo, 1 isquion derecho.

Diagnosis: el esplenial derecho presenta una bifurcación en el límite anterior de su proyección proximal, carácter común en sub-adultos y adultos de *Lacerta* sensu lato [= *Lacerta schreiberi*, *Lacerta bilineata* y *Timon lepidus*] (Barahona, 1996).

Los frontales conservados son grandes, el más grande tiene una longitud de 10 mm, lo cual lo sitúa dentro de los parámetros de *Lacerta* sensu lato (longitud del frontal menor de 9 mm) (Barahona y Barbadillo, 1997). En vista dorsal, los frontales presentan una constricción muy leve en su región medial, como se ha descrito para *L. bilineata* y *L. schreiberi* (Barahona, 1996; Barahona y Barbadillo, 1997).

El parietal de MIR5-P21-n4 permite hacer una asignación más aproximada a nivel específico: en vista ventral el inicio de las crestas ventrales no toca las crestas

posterolaterales (Figura 3.4.I.2), como se ha descrito en adultos de *Psammodromus algirus* y *Lacerta* s.l. (Barahona y Barbadillo, 1997); también en vista ventral presenta una fosa parietal de forma triangular (Figura 3.4.I.2), carácter adscrito a *T. lepidus* y *L. bilineata* (Barahona, 1996). Las medidas del parietal más completo son de 6.6 mm de anchura y 6.8 mm de longitud, en concordancia con lo postulado para *Lacerta* sensu lato (anchura del parietal mayor de 5.7 mm; longitud del parietal mayor de 6 mm) (Barahona y Barbadillo, 1997). Los caracteres descritos son concordantes significativamente con *T. lepidus* y *L. bilineata*, aunque se asignan finalmente a esta última especie por la impresión de la escama occipital sobre la superficie del parietal, que en vista dorsal muestra una extensión reducida sobre el margen posterior del parietal (Figura 3.4.I.1), a diferencia del gran desarrollo que tiene en *T. lepidus* (Barahona, 1996; Barahona y Barbadillo, 1997).

Asimismo, la longitud del cuadrado más completo conservado en MIR5-P21-n4, de lateralidad izquierda, es de 5.1 mm y se sitúa dentro de los parámetros de *Lacerta* sensu lato (longitud del cuadrado mayor de 4 mm) (Figura 3.4.J) (Barahona y Barbadillo, 1997); este mismo cuadrado es el único de los cinco conservados que preserva parcialmente la plataforma anterodorsal, lo cual permite observar en ello una superficie llana en vista lateral (Figura 3.4.J.3), carácter descrito para *L. bilineata* y *L. schreiberi* pero no en los adultos de *T. lepidus*, en los que el cuadrado presenta una superficie cóncava (Barahona, 1996; Barahona y Barbadillo, 1997).

La mayor parte de las vértebras de lacértidos de la muestra han sido asignadas a *Lacerta* cf. *bilineata* por la presencia de una cresta neural marcada que termina en una neuroespina alta de gran desarrollo dorsal y de terminación ancha, hasta llegar en vista dorsal a la altura del cóndilo posterior (Gleed-Owen, 1998). Las vértebras dorsales presentan una longitud del centrum vertebral entre 2.9 y 3.2 mm, muy cercano al valor medio de la longitud marcada para *L. bilineata* (3 mm) (Gleed-Owen, 1998).

Género *Timon* Tschudi, 1836

Timon cf. *lepidus* (Daudin, 1802)

Figura 3.4.K, 4.3.Y

Material examinado:

— MIR4-Q21-n234: 1 parietal fragmentario, 1 surangular izquierdo, 1 surangular derecho.

— MIR4-Q21-n235: 1 dentario izquierdo fragmentario, 1 articular izquierdo fragmentario, 1 parietal fragmentario, 1 surangular derecho, 1 coronoides izquierdo, 1 pterigoides derecho fragmentario, 1 cuadrado derecho, 1 escápula izquierda, 2 vértebras dorsales fragmentarias.

— MIR5-P22-n2: 1 cuadrado izquierdo.

— MIR5-P21-n4: 1 maxilar derecho fragmentario, 1 vértebra cervical.

Diagnosis: los cuadrados conservados son mayores de 4 mm y, aunque parcialmente dañados, presentan una superficie cóncava en la plataforma anterodorsal, carácter propio de los

individuos adultos de *Timon lepidus* (Barahona, 1996; Barahona y Barbadillo, 1997).

Un fragmento de maxilar derecho de lacértido recuperado en MIR5-P21-n4 presenta tres dientes de terminación monocúspide de gran tamaño, de hasta 2.7 mm de longitud desde su arranque, seguidos por un cuarto diente de terminación bicúspide, también de gran tamaño. Este fragmento con solo cuatro dientes tiene una longitud 6.5 mm, lo cual sugiere que se corresponde con un lacértido de muy gran tamaño y con una longitud total de la plataforma dental del maxilar que sobrepasaría ampliamente los 7 mm, medida calculada que lo situaría dentro de los parámetros de *Lacerta* s.l. (Barahona y Barbadillo, 1997). Se ha descrito la presencia en maxilares de individuos de gran tamaño de *T. lepidus*, a partir de la tercera o cuarta posición dental, de dos o tres dientes de mayor tamaño que los del resto de la batería dental, que pueden ser monocúspides o bicúspides (Barahona, 1996).

Además, también se ha identificado MIR5-P21-n4 una vértebra cervical de lacértido de gran tamaño (longitud del centrum ventral: 4.2 mm) (Figura 3.4.K), mucho mayor que las asignadas a cf. *L. bilineata* (longitud del centrum ventral: 2 - 2.2 mm).

El resto de los elementos (incluidos los fragmentarios) en la muestra se asignan a *Timon* cf. *lepidus* por su gran tamaño, que excede lo propio del resto de especies de lacértidos ibérico, comparativamente más pequeños.

Lacertidae indet. (talla pequeña y mediana)

Figura 3.4.G, 4.3.U

Material examinado:

— MIR4-Q21-n227: 1 maxilar derecho fragmentario, 1 vértebra cervical.

— MIR4-Q21-n228: 2 dentarios izquierdos, 1 maxilar derecho fragmentario, 1 parietal fragmentario.

— MIR4-Q21-n245: 1 maxilar derecho fragmentario.

— MIR4-Q20-n261: 1 dentario izquierdo fragmentario.

— MIR4-Q20-n262: 1 vértebra dorsal, 1 vértebra sacra.

— MIR4-P22-n380: 1 dentario izquierdo.

— MIR5-P22-n2: 1 dentario derecho fragmentario, 1 vértebra dorsal.

— MIR5-P21-n4: 1 dentario izquierdo fragmentario, 1 dentario derecho fragmentario, 2 vértebras cervicales, 9 vértebras dorsales, 3 vértebras post-sacrales, 1 parte distal de vértebra caudal, 1 escápula-coracoides izquierdo, 1 ilion izquierdo, 1 ilion derecho, 1 isquion izquierdo, 1 isquion derecho, 1 fémur izquierdo, 1 fémur derecho.

Diagnosis: la identificación en Lacertidae está basada en los dentarios, debido a la presencia de dientes pleurodontes, cilíndricos, huecos y con heterodoncia, con terminaciones monocúspides en las primeras piezas dentales y con dientes bicúspides y tricúspides en las intermedias (Barahona, 1996) (Figura 3.4.G). Estos restos son

atribuidos a lacértidos de pequeño y mediano tamaño, de los que no puede precisarse una mayor asignación taxonómica debido a la falta de caracteres diagnósticos útiles en los restos preservados (Figura 3.4.G). Ocurre en los dentarios identificados que, al no conservar la longitud total de la plataforma dental, no pueden ser utilizados para la diagnosis siguiendo los criterios de Barahona y Barbadillo (1997) (Figura 3.4.G). Tampoco se puede determinar si corresponden a individuos juveniles o adultos.

Familia Colubridae Oppel, 1811

Género *Coronella* Laurenti, 1768

Coronella austriaca Laurenti, 1768

Figuras 3.4.L-M, 4.3.Z-AA

Material examinado:

— MIR4-Q21-n228: 1 vértebra dorsal.

— MIR4-P21-n246: 1 vértebra cervical.

— MIR4-P21-n267: 1 vértebra dorsal.

— MIR5-P22-n1: 2 vértebras dorsales.

— MIR5-P21-n4: 1 dentario izquierdo, 1 dentario derecho, 1 hueso compuesto mandibular izquierdo, 1 hueso compuesto mandibular derecho, 3 vértebras cervicales, 74 vértebras dorsales, 1 vértebra cloacal, 14 vértebras caudales, 14 costillas.

***Diagnosis*:** las vértebras en la muestra asignadas a *C. austriaca* se caracterizan por su reducido tamaño, con una longitud del centrum vertebral que no supera los 2.4 mm (Figura 3.4.M). Las vértebras dorsales presentan en vista ventral una quilla hemal pobremente definida (Figura 3.4.M.2), por lo que se adscriben dentro de la subfamilia Colubrinae (Szyndlar, 1984). El proceso de la prezigapófisis tiene un desarrollo corto en vista ventral (Figura 3.4.M.2), mientras que presenta una neuroespina muy poco desarrollada en vista lateral (Figura 3.4.M.5), a la vez que en vista posterior presenta el arco neural deprimido (Figura 3.4.M.4), caracteres diagnósticos del género *Coronella* (Szyndlar, 1984). La determinación a nivel específico en *C. austriaca* se basa en la presencia, en vista ventral, de unas parapófisis de mayor desarrollo en comparación con las diapófisis (Figura 3.4.M.2) así como por el inicio grueso de las prezigapófisis en su porción proximal, también en vista ventral (Figura 3.4.M.2) (Szyndlar, 1984).

Las vértebras cervicales asignadas a *C. austriaca* presentan hipapófisis en vistas lateral y ventral, de proyección posteroventral.

Las vértebras caudales presentan una neuroespina desarrollada con un saliente anterior y pleurapófisis de mayor desarrollo (0.9 mm) en comparación con las hemapófisis (0.4 mm).

La diferencia de tamaño entre vértebras dorsales, con un conjunto de las cuales presenta una longitud del centrum vertebral de 1.8 mm y otro conjunto con medidas de 2.4 mm, nos sugiere la existencia de como mínimo dos individuos diferentes en MIR5-P21-n4, siendo ambos juveniles, pero uno de ellos más desarrollado que el otro, según los parámetros marcados para la variación intracolumnar de *C. austriaca* por Szyndlar (1984).

Familia Viperidae Oppel, 1811

Género *Vipera* Laurenti, 1768

Vipera sp.

(*Vipera aspis*/*seoanei*)

Figuras 3.4.N, 4.3.AB

Material examinado:

— MIR5-P21-n4: 1 vértebra cervical, 1 vértebra dorsal, 1 vértebra caudal.

***Diagnosis*:** la vértebra cervical asignada a *Vipera* sp. presenta los caracteres diagnósticos de Viperidae: una hipapófisis recta de gran desarrollo, una terminación aguda del proceso de la prezigapófisis y la ausencia de un saliente anterior de la neuroespina en vista lateral, así como un arco neural deprimido posteriormente (Szyndlar, 1984). Tanto la longitud de la hipapófisis (1.2 mm), que es menor a la longitud del centrum vertebral (2.1 mm), así como el escaso desarrollo dorsal de la neuroespina, mucho más larga que alta, permiten descartar su asignación a *V. latastei* (Szyndlar, 1984).

La asignación a nivel específico no puede precisarse debido al estado fragmentario de la vértebra dorsal asignada a *Vipera*. Ésta conserva el inicio de la hipapófisis y la prezigapófisis izquierda, con una terminación aguda de su proceso, pero no se ha conservado el arco neural ni la neuroespina (Figura 3.4.N), lo que habría posibilitado asignar el material de Viperidae a alguna de las restantes especies de víboras ibéricas, *Vipera aspis* o *Vipera seoanei*.

Finalmente, también ha sido adscrita a *Vipera* sp. una vértebra caudal con una neuroespina alargada de escaso desarrollo dorsal y sin saliente anterior, que destaca por la casi igualdad en las longitudes de la pleurapófisis (1.2 mm) y de las hemapófisis (1.1 mm), en contraposición con lo observado en las vértebras caudales asignadas a *C. austriaca*.

Appendix 5 - Data matrix for northern region, including El Mirador

	Rana temporaria-iberica	*Anguis fragilis*	*Bufo gr. Bufo bufo*	*Alytes*	*Salamandra salamandra*	*Epidalea calamita*	*Lacerta*	*Coronella austriaca*	*Natrix maura*	*Natrix natrix s.l.*	*Hyla*	*Malpolon monspessunaluns*	*Chioglossa lusitanica*	*Discoglossus galganoi*	*Chalcides striatus*	*Timon lepidus*	*Ichthyosaura alpestris*	*Lissotriton helveticus*	*Triturus marmoratus*	*Coronella girondica*	*Zamenis longissimus*	*Hierophis viridiflavus*	*Vipera sp. (aspis-seoanei)*	*Zamenis scalaris*	*Pelobates cultripes*	*Vipera latastei*
ASK.13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.8	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASK.1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CND.N104	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CND.N103	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
CND.N10b	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CND.N20a	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
CND.N2a1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CND.N2a2	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COB.7	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COB.6	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COB.5	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COB.4	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COB.3	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COB.2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COB.1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EIR.3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
EIR.2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
POR.16	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.15	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.14	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.13	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.12	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.11	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.10	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
POR.9	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
POR.8	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
POR.7	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
POR.6	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.5	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.4	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.3	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Rana temporaria-iberica	*Anguis fragilis*	*Bufo* gr. *Bufo bufo*	*Alytes*	*Salamandra salamandra*	*Epidalea calamita*	*Lacerta*	*Coronella austriaca*	*Natrix maura*	*Natrix natrix* s.l.	*Hyla*	*Malpolon monspessunaluns*	*Chioglossa lusitanica*	*Discoglossus galganoi*	*Chalcides striatus*	*Timon lepidus*	*Ichthyosaura alpestris*	*Lissotriton helveticus*	*Triturus marmoratus*	*Coronella girondica*	*Zamenis longissimus*	*Hierophis viridiflavus*	*Vipera* sp. (*aspis-seoanei*)	*Zamenis scalaris*	*Pelobates cultripes*	*Vipera latastei*
POR.2	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
POR.1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.D	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.C	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.B	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.A	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAN.Arg-o	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAN.Camr	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
SAN.Csn	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
SAN.Balm	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAN.Almp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAN.Slnc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAN.Arcp	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAN.Slm	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAN.Lsm	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
ERR.VI	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERR.V	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERR.IV	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERR.III	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ERR.II	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VAL.2	1	1	1	0	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
VAL.1	1	1	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0
SCT.III	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
SCT.II	1	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0
SCT.I	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0
LAM.II-I	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
AIZ.15-12	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
MRN 10	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MRN 9	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
MRN 8	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MRN 7	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MRN 6	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MRN 5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MRN 4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
MRN 3	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ORC.II-I	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0
PLR.IV-I	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ETX	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
BLS	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
COL.15	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

	Rana temporaria-iberica	*Anguis fragilis*	*Bufo* gr. *Bufo bufo*	*Alytes*	*Salamandra salamandra*	*Epidalea calamita*	*Lacerta*	*Coronella austriaca*	*Natrix maura*	*Natrix natrix* s.l.	*Hyla*	*Malpolon monspessunaluns*	*Chioglossa lusitanica*	*Discoglossus galganoi*	*Chalcides striatus*	*Timon lepidus*	*Ichthyosaura alpestris*	*Lissotriton helveticus*	*Triturus marmoratus*	*Coronella girondica*	*Zamenis longissimus*	*Hierophis viridiflavus*	*Vipera* sp. (*aspis-seoanei*)	*Zamenis scalaris*	*Pelobates cultripes*	*Vipera latastei*
COL.14-13	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
COL.12	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
COL.EE1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PEV.VI	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PEV.IV	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PEV.III	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PEV.II	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PEV.I	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1
MIR5.pellets	1	1	1	1	0	1	1	1	0	0	1	0	0	0	1	1	0	1	1	0	0	0	1	0	1	0
MIR4.pellets	1	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0

Supplementary Table 5.S1.- Data matrix of the northern regions with significative herpetofaunal assemblages from the latest Pleistocene to the Late Holocene, including El Mirador pellets.

Appendix 6.A - Citas herpetológicas, provincia de Burgos, 2016-2019

Caudata Scopoli, 1777

Familia Salamandridae Goldfuss, 1820

Género *Salamandra* Laurenti, 1768

Salamandra salamandra (Linnaeus, 1758)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Salamandra salamandra	16/6/2017	tarde	18:27	2	larva	activo	arroyo	VN47	VN4373	1096.85	Espinosa de los Monteros
Salamandra salamandra	16/6/2017	tarde	18:33	28	larva	activo	arroyo	VN47	VN4373	1096.98	Espinosa de los Monteros
Salamandra salamandra	19/6/2017	tarde	19:05	1	larva	inactivo	arroyo	VN47	VN4977	1006.02	Lunada
Salamandra salamandra	19/6/2017	tarde	19:05	1	larva	inactivo	arroyo	VN47	VN4977	1006.18	Lunada
Salamandra salamandra	19/6/2017	tarde	18:57	1	larva	activo	arroyo	VN47	VN4977	1009.96	Lunada
Salamandra salamandra	19/6/2017	tarde	18:54	1	larva	inactivo	arroyo	VN47	VN4977	1010.53	Lunada
Salamandra salamandra	19/6/2017	tarde	18:51	1	larva	activo	arroyo	VN47	VN4977	1011.18	Lunada
Salamandra salamandra	19/6/2017	tarde	18:51	1	larva	activo	arroyo	VN47	VN4977	1010.91	Lunada
Salamandra salamandra	19/6/2017	tarde	18:49	1	larva	activo	arroyo	VN47	VN4977	1010.23	Lunada
Salamandra salamandra	21/6/2017	mediodía	12:33	22	larva	activo	rio o canal	VN95	VN9954	836.00	Monte Santiago
Salamandra salamandra	24/6/2017	mediodía	12:21	9	larva	activo	arroyo	VN47	VN4671	1309.68	Espinosa de los Monteros
Salamandra salamandra	24/6/2017	mañana	10:20	26	larva	activo	arroyo	VN47	VN4671	1313.67	Espinosa de los Monteros
Salamandra salamandra	8/4/2019	noche	01:16	63	larva	activo	charca	VN12	VN1125	956.49	Humada
Salamandra salamandra	8/4/2019	mañana	11:49	1	metamórfico	activo	balsa	VN25	VN2857	909.81	Villamediana de San Román
Salamandra salamandra	8/4/2019	mañana	11:49	1	larva	activo	balsa	VN25	VN2857	909.79	Villamediana de San Román
Salamandra salamandra	8/4/2019	mañana	11:48	1	metamórfico	activo	balsa	VN25	VN2857	909.80	Villamediana de San Román
Salamandra salamandra	8/4/2019	mañana	11:48	1	metamórfico	activo	balsa	VN25	VN2857	909.79	Villamediana de San Román
Salamandra salamandra	4/7/2019	mañana	09:08	30	larva	activo	arroyo	VN47	VN4573	1008.37	Espinosa de los Monteros
Salamandra salamandra	4/7/2019	tarde	13:50	50	larva	activo	arroyo	VN47	VN4372	1096.17	Espinosa de los Monteros

Género *Triturus* Rafinesque, 1815

Triturus marmoratus (Latreille, 1800)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Triturus marmoratus	2/7/2016	tarde	19:24	11	adulto	inactivo	matorral de montaña	VM58	VM5788	1002.41	Ibeas de Juarros
Triturus marmoratus	13/7/2016	tarde	19:02	1	adulto	inactivo	bosque de ribera	VM59	VM5892	939.90	Atapuerca
Triturus marmoratus	13/7/2016	tarde	18:52	2	adulto	inactivo	bosque de ribera	VM59	VM5892	939.58	Atapuerca
Triturus marmoratus	14/7/2016	mediodía	11:11	4	adulto	inactivo	charca	VM58	VM5987	1010.81	Zalduendo
Triturus marmoratus	14/7/2016	mediodía	11:18	1	joven	inactivo	charca	VM58	VM5987	1010.81	Zalduendo
Triturus marmoratus	17/6/2017	mediodía	12:04	18	larva	activo	balsa	VN87	VN8577	239.34	Orrantia, Ayega
Triturus marmoratus	17/6/2017	mañana	11:57	15	larva	activo	balsa	VN87	VN8577	238.89	Orrantia, Ayega
Triturus marmoratus	20/6/2017	noche	23:51	1	adulto	activo	lago o pantano	VN42	VN4820	982.07	Cernégula
Triturus marmoratus	20/6/2017	noche	23:02	1	adulto	activo	balsa	VN42	VN4821	982.40	Cernégula
Triturus marmoratus	20/6/2017	noche	22:57	1	adulto	activo	balsa	VN42	VN4821	982.02	Cernégula
Triturus marmoratus	20/6/2017	atardecer	21:56	1	adulto	activo	lago o pantano	VN42	VN4622	1013.08	Cernégula
Triturus marmoratus	20/6/2017	mediodía	13:19	1	adulto	inactivo	cantera	VM58	VM5788	1000.63	Ibeas de Juarros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Triturus marmoratus	20/6/2017	mediodía	13:18	1	adulto	inactivo	cantera	VM58	VM5788	1000.26	Ibeas de Juarros
Triturus marmoratus	20/6/2017	mediodía	13:16	1	adulto	inactivo	cantera	VM58	VM5788	1000.13	Ibeas de Juarros
Triturus marmoratus	21/6/2017	tarde	19:55	1	adulto	activo	balsa	VN95	VN9854	902.06	Monte Santiago
Triturus marmoratus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.33	Atapuerca
Triturus marmoratus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.51	Atapuerca
Triturus marmoratus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.51	Atapuerca
Triturus marmoratus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.54	Atapuerca
Triturus marmoratus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.48	Atapuerca
Triturus marmoratus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.42	Atapuerca
Triturus marmoratus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.42	Atapuerca
Triturus marmoratus	24/6/2017	tarde	17:52	1	larva	activo	balsa	VN35	VN3458	824.88	Soncillo
Triturus marmoratus	24/6/2017	tarde	14:13	1	adulto	inactivo	balsa	VN46	VN4668	941.44	Quisicedo
Triturus marmoratus	24/6/2017	tarde	14:13	1	adulto	inactivo	balsa	VN46	VN4668	941.44	Quisicedo
Triturus marmoratus	24/6/2017	tarde	14:12	1	adulto	inactivo	balsa	VN46	VN4668	941.36	Quisicedo
Triturus marmoratus	24/6/2017	tarde	14:11	1	adulto	activo	balsa	VN46	VN4668	941.27	Quisicedo
Triturus marmoratus	24/6/2017	tarde	14:09	1	adulto	activo	balsa	VN46	VN4668	940.98	Quisicedo
Triturus marmoratus	25/6/2017	tarde	15:31	1	adulto	activo	balsa	VN42	VN4821	981.97	Cernégula
Triturus marmoratus	27/6/2017	tarde	15:29	1	adulto	activo	balsa	VN43	VN4033	1007.26	Nocedo
Triturus marmoratus	27/6/2017	tarde	15:27	1	adulto	activo	balsa	VN43	VN4033	1007.14	Nocedo
Triturus marmoratus	27/6/2017	tarde	15:27	1	adulto	activo	balsa	VN43	VN4033	1007.20	Nocedo
Triturus marmoratus	27/6/2017	tarde	15:25	1	adulto	inactivo	balsa	VN43	VN4033	1007.25	Nocedo
Triturus marmoratus	28/6/2017	atardecer	23:14	1	adulto	activo	balsa	VN22	VN2122	984.52	Talamillo del Tozo
Triturus marmoratus	28/6/2017	atardecer	21:28	1	joven	inactivo	bosque de ribera	VN22	VN2122	984.11	Talamillo del Tozo
Triturus marmoratus	28/6/2017	atardecer	21:28	1	joven	inactivo	bosque de ribera	VN22	VN2122	984.04	Talamillo del Tozo
Triturus marmoratus	28/6/2017	tarde	18:30	1	larva	activo	balsa	VN23	VN2833	1008.94	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:29	1	larva	activo	balsa	VN23	VN2833	1008.93	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:28	1	larva	activo	balsa	VN23	VN2833	1008.91	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:28	1	larva	activo	balsa	VN23	VN2833	1008.93	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:23	1	larva	activo	balsa	VN23	VN2833	1009.06	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:15	1	larva	activo	balsa	VN23	VN2833	1009.74	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:22	1	larva	activo	balsa	VN23	VN2833	1009.26	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:31	1	metamórfico	activo	balsa	VN23	VN2833	1009.05	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:13	2	larva	activo	balsa	VN23	VN2833	1009.36	Ayoluengo
Triturus marmoratus	28/6/2017	tarde	18:09	1	larva	activo	balsa	VN23	VN2833	1009.25	Ayoluengo
Triturus marmoratus	2/7/2017	mañana	08:51	3	adulto	inactivo	cantera	VM58	VM5788	1004.08	Ibeas de Juarros
Triturus marmoratus	6/4/2019	mediodía	12:02	1	adulto	inactivo	robledal marcescente	VN12	VN1827	919.17	Basconcillos del Tozo
Triturus marmoratus	7/4/2019	atardecer	19:35	1	adulto	activo	balsa	VN43	VN4033	1007.11	Nocedo
Triturus marmoratus	7/4/2019	atardecer	19:35	1	adulto	activo	balsa	VN43	VN4033	1007.18	Nocedo
Triturus marmoratus	7/4/2019	atardecer	19:36	1	adulto	activo	balsa	VN43	VN4033	1007.28	Nocedo
Triturus marmoratus	8/4/2019	noche	01:16	1	adulto	activo	robledal marcescente	VN12	VN1125	955.01	Humada
Triturus marmoratus	8/4/2019	noche	01:21	1	adulto	activo	robledal marcescente	VN12	VN1125	952.91	Humada
Triturus marmoratus	8/4/2019	noche	01:23	1	adulto	activo	robledal marcescente	VN12	VN1125	951.66	Humada
Triturus marmoratus	19/6/2019	mañana	09:09	1	joven	inactivo	cantera	VM58	VM5788	1006.01	Ibeas de Juarros
Triturus marmoratus	19/6/2019	mañana	09:09	1	joven	inactivo	cantera	VM58	VM5788	1005.06	Ibeas de Juarros
Triturus marmoratus	5/7/2019	mañana	09:11	1	joven	activo	matorral de montaña	VN25	VN2658	894.46	Herbosa

Género *Ichthyosaura* Sonnini de Manoncourt & Latreille, 1801

Ichthyosaura alpestris (Laurenti, 1768)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Ichthyosaura alpestris	16/6/2017	tarde	15:55	3	adulto	activo	arroyo	VN47	VN4373	1120.55	Espinosa de los Monteros
Ichthyosaura alpestris	16/6/2017	tarde	15:55	1	adulto	activo	arroyo	VN47	VN4373	1120.66	Espinosa de los Monteros
Ichthyosaura alpestris	16/6/2017	tarde	15:47	1	adulto	activo	arroyo	VN47	VN4373	1120.77	Espinosa de los Monteros
Ichthyosaura alpestris	16/6/2017	tarde	15:47	1	adulto	inactivo	arroyo	VN47	VN4373	1120.77	Espinosa de los Monteros
Ichthyosaura alpestris	16/6/2017	tarde	14:27	1	adulto	activo	arroyo	VN47	VN4373	1094.55	Espinosa de los Monteros
Ichthyosaura alpestris	16/6/2017	tarde	14:26	1	adulto	activo	arroyo	VN47	VN4373	1094.49	Espinosa de los Monteros
Ichthyosaura alpestris	19/6/2017	tarde	18:58	1	adulto	inactivo	arroyo	VN47	VN4977	1011.94	Lunada
Ichthyosaura alpestris	19/6/2017	tarde	18:56	1	adulto	activo	arroyo	VN47	VN4977	1011.67	Lunada
Ichthyosaura alpestris	19/6/2017	tarde	18:56	1	adulto	inactivo	arroyo	VN47	VN4977	1011.48	Lunada
Ichthyosaura alpestris	19/6/2017	tarde	18:52	1	adulto	activo	arroyo	VN47	VN4977	1011.12	Lunada
Ichthyosaura alpestris	19/6/2017	tarde	18:49	1	adulto	activo	arroyo	VN47	VN4977	1010.22	Lunada
Ichthyosaura alpestris	19/6/2017	tarde	18:46	1	adulto	inactivo	arroyo	VN47	VN4977	1010.72	Lunada
Ichthyosaura alpestris	19/6/2017	tarde	18:46	1	adulto	activo	arroyo	VN47	VN4977	1010.45	Lunada
Ichthyosaura alpestris	19/6/2017	tarde	18:44	1	adulto	activo	arroyo	VN47	VN4977	1010.29	Lunada
Ichthyosaura alpestris	21/6/2017	mediodía	12:33	11	adulto	activo	rio o canal	VN95	VN9954	836.32	Monte Santiago
Ichthyosaura alpestris	6/4/2019	atardecer	19:57	1	adulto	activo	balsa	VN25	VN2658	877.24	Herbosa
Ichthyosaura alpestris	8/4/2019	mañana	11:48	1	adulto	activo	balsa	VN25	VN2857	909.79	Villamediana de San Román
Ichthyosaura alpestris	8/4/2019	mañana	11:48	1	adulto	activo	balsa	VN25	VN2857	909.80	Villamediana de San Román
Ichthyosaura alpestris	8/4/2019	mañana	11:49	1	adulto	activo	balsa	VN25	VN2857	909.79	Villamediana de San Román
Ichthyosaura alpestris	8/4/2019	mañana	11:49	1	adulto	activo	balsa	VN25	VN2857	909.81	Villamediana de San Román
Ichthyosaura alpestris	8/4/2019	mañana	11:49	1	adulto	activo	balsa	VN25	VN2857	909.81	Villamediana de San Román
Ichthyosaura alpestris	8/4/2019	mañana	11:48	1	adulto	activo	balsa	VN25	VN2857	909.80	Villamediana de San Román
Ichthyosaura alpestris	4/7/2019	mañana	09:53	1	adulto	activo	arroyo	VN47	VN4373	1120.22	Espinosa de los Monteros
Ichthyosaura alpestris	4/7/2019	mañana	09:42	1	adulto	activo	arroyo	VN47	VN4373	1120.12	Espinosa de los Monteros
Ichthyosaura alpestris	4/7/2019	tarde	13:50	1	adulto	activo	arroyo	VN47	VN4373	1097.30	Espinosa de los Monteros
Ichthyosaura alpestris	4/7/2019	atardecer	22:07	1	adulto	activo	balsa	VN25	VN2658	877.36	Herbosa
Ichthyosaura alpestris	4/7/2019	atardecer	22:08	1	adulto	activo	balsa	VN25	VN2658	877.24	Herbosa

Género *Lissotriton* Bell, 1839

Lissotriton helveticus (Razoumowsky, 1789)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Lissotriton helveticus	2/7/2016	tarde	19:24	1	adulto	inactivo	matorral de montaña	VM58	VM5788	1002.41	Ibeas de Juarros
Lissotriton helveticus	13/7/2016	tarde	19:02	5	adulto	inactivo	bosque de ribera	VM59	VM5892	939.90	Atapuerca
Lissotriton helveticus	13/7/2016	tarde	18:52	5	adulto	inactivo	bosque de ribera	VM59	VM5892	939.58	Atapuerca
Lissotriton helveticus	16/6/2017	tarde	18:59	2	adulto	activo	charca	VN47	VN4272	1196.41	Espinosa de los Monteros
Lissotriton helveticus	16/6/2017	tarde	18:58	1	adulto	activo	charca	VN47	VN4272	1197.74	Espinosa de los Monteros
Lissotriton helveticus	16/6/2017	tarde	18:18	1	adulto	alimentación	arroyo	VN47	VN4373	1096.93	Espinosa de los Monteros
Lissotriton helveticus	16/6/2017	tarde	18:18	4	adulto	canto y/o cortejo	arroyo	VN47	VN4373	1096.81	Espinosa de los Monteros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Lissotriton helveticus	16/6/2017	tarde	18:18	23	adulto	activo	arroyo	VN47	VN4373	1096.81	Espinosa de los Monteros
Lissotriton helveticus	16/6/2017	mediodía	13:28	2	adulto	activo	rio o canal	VN47	VN4373	1124.74	Espinosa de los Monteros
Lissotriton helveticus	16/6/2017	mediodía	13:30	1	adulto	activo	rio o canal	VN47	VN4274	1149.70	Espinosa de los Monteros
Lissotriton helveticus	16/6/2017	mediodía	12:02	4	adulto	canto y/o cortejo	arroyo	VN47	VN4574	1019.96	Espinosa de los Monteros
Lissotriton helveticus	16/6/2017	mediodía	12:02	8	adulto	activo	arroyo	VN47	VN4574	1020.01	Espinosa de los Monteros
Lissotriton helveticus	17/6/2017	mediodía	12:04	5	larva	activo	balsa	VN87	VN8577	239.36	Orrantia, Ayega
Lissotriton helveticus	17/6/2017	mediodía	12:04	1	adulto	inactivo	balsa	VN87	VN8577	239.76	Orrantia, Ayega
Lissotriton helveticus	17/6/2017	mañana	11:57	2	larva	activo	balsa	VN87	VN8577	238.89	Orrantia, Ayega
Lissotriton helveticus	18/6/2017	noche	23:37	2	adulto	activo	balsa	VN56	VN5668	731.60	Espinosa de los Monteros
Lissotriton helveticus	18/6/2017	noche	23:37	4	adulto	activo	balsa	VN56	VN5668	731.60	Espinosa de los Monteros
Lissotriton helveticus	18/6/2017	tarde	19:22	1	adulto	inactivo	balsa	VN36	VN3664	807.28	Busnela
Lissotriton helveticus	18/6/2017	tarde	19:22	30	larva	activo	balsa	VN36	VN3664	807.35	Busnela
Lissotriton helveticus	19/6/2017	noche	23:52	12	larva	activo	balsa	VN56	VN5569	746.77	Espinosa de los Monteros
Lissotriton helveticus	19/6/2017	tarde	19:06	1	larva	activo	arroyo	VN47	VN4977	1005.52	Lunada
Lissotriton helveticus	19/6/2017	tarde	18:58	1	adulto	activo	arroyo	VN47	VN4977	1009.19	Lunada
Lissotriton helveticus	21/6/2017	tarde	19:52	1	adulto	activo	balsa	VN95	VN9854	901.88	Monte Santiago
Lissotriton helveticus	21/6/2017	tarde	19:51	1	adulto	activo	balsa	VN95	VN9854	902.43	Monte Santiago
Lissotriton helveticus	21/6/2017	mediodía	12:33	8	adulto	canto y/o cortejo	rio o canal	VN95	VN9954	836.60	Monte Santiago
Lissotriton helveticus	21/6/2017	mediodía	12:33	25	adulto	activo	rio o canal	VN95	VN9954	837.04	Monte Santiago
Lissotriton helveticus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.62	Atapuerca
Lissotriton helveticus	22/6/2017	tarde	19:11	1	joven	inactivo	bosque de ribera	VM59	VM5892	939.62	Atapuerca
Lissotriton helveticus	24/6/2017	tarde	17:54	1	larva	activo	balsa	VN35	VN3458	824.54	Soncillo
Lissotriton helveticus	24/6/2017	tarde	14:13	1	adulto	activo	balsa	VN46	VN4668	941.42	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:13	1	adulto	activo	balsa	VN46	VN4668	941.44	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:13	1	adulto	inactivo	balsa	VN46	VN4668	941.36	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:12	1	adulto	inactivo	balsa	VN46	VN4668	941.51	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:12	1	adulto	inactivo	balsa	VN46	VN4668	941.36	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:12	1	adulto	activo	balsa	VN46	VN4668	941.27	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:12	1	adulto	activo	balsa	VN46	VN4668	941.12	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:11	1	adulto	activo	balsa	VN46	VN4668	941.27	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:11	1	adulto	activo	balsa	VN46	VN4668	941.34	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:11	1	adulto	activo	balsa	VN46	VN4668	940.87	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:11	1	adulto	activo	balsa	VN46	VN4668	941.12	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:10	1	adulto	activo	balsa	VN46	VN4668	941.27	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:09	1	adulto	activo	balsa	VN46	VN4668	941.27	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:09	1	adulto	inactivo	balsa	VN46	VN4668	941.22	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:09	1	adulto	inactivo	balsa	VN46	VN4668	941.05	Quisicedo
Lissotriton helveticus	24/6/2017	tarde	14:10	1	adulto	activo	balsa	VN46	VN4668	941.42	Quisicedo
Lissotriton helveticus	26/6/2017	mediodía	12:51	1	adulto	inactivo	prado o pasto	VN56	VN5768	721.58	Espinosa de los Monteros
Lissotriton helveticus	26/6/2017	mediodía	12:49	1	adulto	inactivo	prado o pasto	VN56	VN5768	721.63	Espinosa de los Monteros
Lissotriton helveticus	26/6/2017	mediodía	12:49	1	adulto	inactivo	prado o pasto	VN56	VN5768	721.50	Espinosa de los Monteros
Lissotriton helveticus	7/4/2019	tarde	17:42	1	adulto	activo	arroyo	VN36	VN3664	806.91	Busnela
Lissotriton helveticus	7/4/2019	tarde	17:42	1	adulto	activo	arroyo	VN36	VN3664	806.23	Busnela

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Lissotriton helveticus	7/4/2019	tarde	17:42	1	adulto	activo	arroyo	VN36	VN3664	806.25	Busnela
Lissotriton helveticus	7/4/2019	tarde	17:42	1	adulto	activo	arroyo	VN36	VN3664	806.68	Busnela
Lissotriton helveticus	7/4/2019	tarde	17:41	1	adulto	activo	arroyo	VN36	VN3664	806.81	Busnela
Lissotriton helveticus	7/4/2019	tarde	17:41	1	adulto	activo	arroyo	VN36	VN3664	807.24	Busnela
Lissotriton helveticus	7/4/2019	atardecer	19:36	1	adulto	activo	balsa	VN43	VN4033	1007.20	Nocedo
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	activo	arroyo	VN47	VN4373	1097.06	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	activo	arroyo	VN47	VN4373	1097.03	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	activo	arroyo	VN47	VN4373	1096.81	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	activo	arroyo	VN47	VN4372	1096.29	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4372	1095.87	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4372	1095.87	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4372	1096.01	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4372	1096.01	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4373	1096.72	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4373	1096.72	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4373	1097.42	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4373	1097.42	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4372	1096.42	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4372	1096.42	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4373	1097.04	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	tarde	13:50	1	adulto	canto y/o cortejo	arroyo	VN47	VN4373	1097.04	Espinosa de los Monteros
Lissotriton helveticus	4/7/2019	atardecer	22:02	100	larva	activo	balsa	VN25	VN2658	877.26	Herbosa
Lissotriton helveticus	4/7/2019	atardecer	22:08	1	adulto	activo	balsa	VN25	VN2658	877.25	Herbosa

Anura Rafinesque, 1815

Familia Alytidae Fitzinger, 1843

Género *Alytes* Wagler, 1829

Alytes obstetricans (Laurenti, 1768)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Alytes obstetricans	15/6/2017	noche	23:33	9	adulto	canto y/o cortejo	bosque de ribera	VN56	VN5767	715.85	Espinosa de los Monteros
Alytes obstetricans	16/6/2017	tarde	18:19	20	metamórfico	activo	arroyo	VN47	VN4373	1096.58	Espinosa de los Monteros
Alytes obstetricans	16/6/2017	tarde	18:19	50	larva	activo	arroyo	VN47	VN4372	1096.45	Espinosa de los Monteros
Alytes obstetricans	16/6/2017	mediodía	12:02	15	larva	activo	arroyo	VN47	VN4574	1020.35	Espinosa de los Monteros
Alytes obstetricans	16/6/2017	mañana	11:32	20	larva	activo	arroyo	VN47	VN4574	1029.26	Espinosa de los Monteros
Alytes obstetricans	16/6/2017	noche	00:37	1	adulto	canto y/o cortejo	bosque de ribera	VN56	VN5469	741.35	Espinosa de los Monteros
Alytes obstetricans	17/6/2017	mediodía	12:31	25	larva	activo	charca	VN87	VN8678	187.54	Arza, Ayega
Alytes obstetricans	17/6/2017	mediodía	12:28	30	larva	activo	charca	VN87	VN8678	187.43	Arza, Ayega
Alytes obstetricans	17/6/2017	mediodía	12:04	50	larva	activo	balsa	VN87	VN8577	239.48	Orrantia, Ayega
Alytes obstetricans	17/6/2017	mañana	11:57	30	larva	activo	balsa	VN87	VN8577	238.92	Orrantia, Ayega
Alytes obstetricans	17/6/2017	mañana	10:31	60	larva	activo	arroyo	VN87	VN8076	275.48	Opio

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Alytes obstetricans	18/6/2017	noche	23:35	8	metamórfico	activo	balsa	VN56	VN5668	732.34	Espinosa de los Monteros
Alytes obstetricans	18/6/2017	noche	23:35	30	larva	activo	balsa	VN56	VN5668	732.44	Espinosa de los Monteros
Alytes obstetricans	18/6/2017	tarde	19:22	100	larva	activo	balsa	VN36	VN3664	807.22	Busnela
Alytes obstetricans	19/6/2017	noche	23:51	1	adulto	canto y/o cortejo	bosque de ribera	VN56	VN5569	748.48	Espinosa de los Monteros
Alytes obstetricans	19/6/2017	noche	23:30	1	adulto	canto y/o cortejo	bosque de ribera	VN56	VN5668	719.04	Espinosa de los Monteros
Alytes obstetricans	19/6/2017	tarde	19:04	1	larva	activo	arroyo	VN47	VN4977	1006.75	Lunada
Alytes obstetricans	19/6/2017	mañana	10:28	100	larva	activo	rio o canal	VN67	VN6373	801.49	Agüera
Alytes obstetricans	19/6/2017	mañana	10:26	50	larva	activo	rio o canal	VN67	VN6373	804.88	Agüera
Alytes obstetricans	20/6/2017	atardecer	22:31	1	adulto	canto y/o cortejo	prado o pasto	VN42	VN4622	1016.81	Cernégula
Alytes obstetricans	20/6/2017	atardecer	22:25	1	larva	activo	lago o pantano	VN42	VN4622	1013.07	Cernégula
Alytes obstetricans	20/6/2017	noche	01:20	1	adulto	canto y/o cortejo	bosque de ribera	VN56	VN5667	723.46	Espinosa de los Monteros
Alytes obstetricans	21/6/2017	tarde	20:53	1	adulto	muerto	prado o pasto	VN95	VN9754	873.28	Monte Santiago
Alytes obstetricans	21/6/2017	tarde	20:48	1	adulto	inactivo	prado o pasto	VN95	VN9753	869.24	Monte Santiago
Alytes obstetricans	21/6/2017	tarde	20:02	50	larva	activo	balsa	VN95	VN9854	902.67	Monte Santiago
Alytes obstetricans	21/6/2017	tarde	19:51	1	adulto	canto y/o cortejo	prado o pasto	VN95	VN9854	914.36	Monte Santiago
Alytes obstetricans	21/6/2017	tarde	19:43	1	metamórfico	inactivo	prado o pasto	VN95	VN9854	903.58	Monte Santiago
Alytes obstetricans	21/6/2017	mediodía	12:33	100	larva	activo	rio o canal	VN95	VN9954	836.68	Monte Santiago
Alytes obstetricans	21/6/2017	noche	00:10	1	adulto	activo	cultivo de secano	VN42	VN4821	984.98	Cernégula
Alytes obstetricans	21/6/2017	noche	00:07	1	adulto	activo	matorral mediterráneo	VN42	VN4821	983.31	Cernégula
Alytes obstetricans	21/6/2017	noche	00:04	1	adulto	activo	prado o pasto	VN42	VN4820	982.57	Cernégula
Alytes obstetricans	21/6/2017	noche	00:01	1	adulto	canto y/o cortejo	cultivo de regadío	VN42	VN4820	979.80	Cernégula
Alytes obstetricans	22/6/2017	noche	22:47	1	adulto	activo	cultivo de secano	VN40	VN4406	955.93	Gredilla la Polera
Alytes obstetricans	22/6/2017	noche	22:55	1	adulto	canto y/o cortejo	bosque de ribera	VN40	VN4407	896.43	Gredilla la Polera
Alytes obstetricans	23/6/2017	mediodía	13:03	150	larva	activo	balsa	VN43	VN4433	1047.43	Huidobro
Alytes obstetricans	24/6/2017	tarde	17:53	1	larva	activo	balsa	VN35	VN3458	824.96	Soncillo
Alytes obstetricans	24/6/2017	tarde	17:16	8	metamórfico	activo	charca	VN35	VN3657	839.60	Soncillo
Alytes obstetricans	24/6/2017	tarde	17:16	50	larva	activo	charca	VN35	VN3657	839.56	Soncillo
Alytes obstetricans	24/6/2017	tarde	14:13	1	metamórfico	activo	balsa	VN46	VN4668	941.36	Quisicedo
Alytes obstetricans	24/6/2017	tarde	14:05	200	larva	activo	balsa	VN46	VN4668	945.74	Quisicedo
Alytes obstetricans	26/6/2017	tarde	16:21	50	larva	activo	rio o canal	VN56	VN5768	715.05	Espinosa de los Monteros
Alytes obstetricans	27/6/2017	tarde	16:55	155	larva	activo	balsa	VN43	VN4033	1007.26	Nocedo
Alytes obstetricans	27/6/2017	tarde	15:31	1	larva	activo	balsa	VN43	VN4033	1007.21	Nocedo
Alytes obstetricans	28/6/2017	atardecer	21:43	50	larva	activo	arroyo	VN22	VN2022	998.68	Talamillo del Tozo
Alytes obstetricans	28/6/2017	atardecer	21:32	1	larva	activo	balsa	VN22	VN2122	984.52	Talamillo del Tozo
Alytes obstetricans	28/6/2017	tarde	18:47	150	larva	activo	balsa	VN23	VN2933	1027.63	Ayoluengo,
Alytes obstetricans	28/6/2017	tarde	18:23	1	larva	activo	balsa	VN23	VN2833	1009.06	Ayoluengo
Alytes obstetricans	28/6/2017	tarde	18:15	1	larva	activo	balsa	VN23	VN2833	1009.68	Ayoluengo
Alytes obstetricans	30/6/2017	tarde	14:52	200	larva	activo	balsa	VN52	VN5824	742.84	Poza de la Sal
Alytes obstetricans	30/6/2017	tarde	14:49	200	larva	activo	balsa	VN52	VN5824	743.82	Poza de la Sal
Alytes obstetricans	30/6/2017	tarde	18:35	1	adulto	muerto	matorral mediterráneo	VN51	VN5919	655.01	Lences
Alytes obstetricans	6/4/2019	mañana	11:36	1	adulto	inactivo	prado o pasto	VN12	VN1827	914.68	Basconcillos del Tozo
Alytes obstetricans	7/4/2019	atardecer	19:38	26	larva	activo	balsa	VN43	VN4033	1007.21	Nocedo, Valle de Sedano.
Alytes obstetricans	3/7/2019	noche	22:30	10	adulto	canto y/o cortejo	bosque de ribera	VN56	VN5768	715.65	Espinosa de los Monteros.
Alytes obstetricans	21/6/2019	noche	00:49	1	adulto	activo	balsa	VN42	VN4821	987.13	Cernégula

Familia Pelobatidae Bonaparte, 1850

Género *Pelobates* Wagler, 1830

Pelobates cultripes (Cuvier, 1829)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Pelobates cultripes	21/6/2019	noche	00:22	1	joven	activo	cultivo de secano	VN42	VN4524	1000.46	Cernégula
Pelobates cultripes	21/6/2019	noche	00:27	1	joven	activo	cultivo de secano	VN42	VN4524	999.94	Cernégula

Familia Pelodytidae Bonaparte, 1850

Género *Pelodytes* Bonaparte, 1838

Pelodytes punctatus (Daudin, 1802)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Pelodytes punctatus	2/7/2016	tarde	19:24	2	adulto	inactivo	matorral de montaña	VM58	VM5788	1002.41	Ibeas de Juarros
Pelodytes punctatus	8/7/2016	tarde	16:44	1	joven	inactivo	matorral de montaña	VM58	VM5788	1002.41	Ibeas de Juarros
Pelodytes punctatus	6/7/2017	mañana	9:33	1	adulto	escape	cantera	VM58	VM5887	1039.83	Ibeas de Juarros
Pelodytes punctatus	16/7/2017	mediodía	12:12	1	joven	activo	cantera	VM58	VM5788	1005.50	Ibeas de Juarros
Pelodytes punctatus	8/4/2019	noche	01:36	1	adulto	activo	charca	VN12	VN1124	946.12	Humada
Pelodytes punctatus	8/4/2019	noche	01:49	1	adulto	activo	charca	VN12	VN1124	944.20	Humada

Familia Bufonidae Laurenti, 1768

Género *Bufo* Laurenti, 1768

Bufo spinosus Daudin, 1803

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Bufo spinosus	8/7/2016	tarde	16:44	1	joven	inactivo	matorral de montaña	VM58	VM5788	1002.41	Ibeas de Juarros
Bufo spinosus	9/7/2016	mediodía	12:19	1	adulto	Atropellado	bosque de ribera	VN52	VN5920	659.80	Lences
Bufo spinosus	16/5/2017	mediodía	13:47	1	metamórfico	activo	turbera	VN47	VN4373	1111.89	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	23:24	1	adulto	activo	prado o pasto	VN56	VN5768	715.96	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	23:23	1	adulto	activo	prado o pasto	VN56	VN5768	717.93	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	23:13	1	adulto	inactivo	hayedo, robledal o frondosas	VN56	VN5668	729.80	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	22:53	1	adulto	activo	hayedo, robledal o frondosas	VN56	VN5668	732.97	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	22:42	1	adulto	activo	hayedo, robledal o frondosas	VN56	VN5668	733.22	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	22:37	1	adulto	activo	hayedo, robledal o frondosas	VN56	VN5668	733.23	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	22:26	1	adulto	activo	hayedo, robledal o frondosas	VN56	VN5668	733.90	Espinosa de los Monteros
Bufo spinosus	15/6/2017	noche	22:23	1	adulto	activo	hayedo, robledal o frondosas	VN56	VN5668	734.02	Espinosa de los Monteros
Bufo spinosus	16/6/2017	atardecer	20:39	8	metamórfico	activo	charca	VN47	VN4774	969.81	Espinosa de los Monteros
Bufo spinosus	16/6/2017	atardecer	20:39	100	larva	activo	charca	VN47	VN4774	969.76	Espinosa de los Monteros
Bufo spinosus	16/6/2017	tarde	16:52	30	larva	activo	arroyo	VN47	VN4373	1101.94	Espinosa de los Monteros
Bufo spinosus	16/6/2017	tarde	16:52	20	larva	activo	arroyo	VN47	VN4373	1103.33	Espinosa de los Monteros
Bufo spinosus	16/6/2017	tarde	16:50	25	larva	activo	arroyo	VN47	VN4373	1106.16	Espinosa de los Monteros
Bufo spinosus	16/6/2017	tarde	16:13	1	adulto	activo	arroyo	VN47	VN4373	1120.08	Espinosa de los Monteros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Bufo spinosus	16/6/2017	tarde	14:17	2	adulto	activo	turbera	VN47	VN4373	1096.25	Espinosa de los Monteros
Bufo spinosus	16/6/2017	tarde	14:16	1	adulto	inactivo	turbera	VN47	VN4373	1096.16	Espinosa de los Monteros
Bufo spinosus	16/6/2017	tarde	14:16	1	metamórfico	inactivo	turbera	VN47	VN4373	1096.17	Espinosa de los Monteros
Bufo spinosus	16/6/2017	tarde	14:04	1	joven	activo	turbera	VN47	VN4373	1112.45	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mediodía	13:56	40	larva	activo	arroyo	VN47	VN4373	1116.22	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mediodía	12:02	200	larva	activo	arroyo	VN47	VN4574	1019.71	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mañana	11:32	100	larva hibernante	activo	arroyo	VN47	VN4574	1029.86	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mañana	10:57	100	larva	activo	arroyo	VN47	VN4574	1003.11	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mañana	10:56	1	metamórfico	activo	prado o pasto	VN47	VN4574	1004.62	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mañana	10:49	1	metamórfico	activo	prado o pasto	VN47	VN4573	1007.24	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mañana	10:38	100	larva		arroyo	VN47	VN4573	1003.84	Espinosa de los Monteros
Bufo spinosus	16/6/2017	mañana	10:36	100	larva	activo	arroyo	VN47	VN4573	1007.53	Espinosa de los Monteros
Bufo spinosus	16/6/2017	noche	00:10	1	adulto	inactivo	rio o canal	VN56	VN5469	744.93	Espinosa de los Monteros
Bufo spinosus	18/6/2017	tarde	15:40	100	larva	activo	rio o canal	VN46	VN4666	719.70	Quisicedo
Bufo spinosus	19/6/2017	noche	23:59	1	adulto	activo	prado o pasto	VN56	VN5469	755.10	Espinosa de los Monteros
Bufo spinosus	19/6/2017	noche	23:57	1	adulto	activo	prado o pasto	VN56	VN5569	750.07	Espinosa de los Monteros
Bufo spinosus	19/6/2017	noche	23:44	1	adulto	activo	prado o pasto	VN56	VN5568	740.07	Espinosa de los Monteros
Bufo spinosus	19/6/2017	noche	23:26	1	adulto	activo	hayedo, robledal o frondosas	VN56	VN5668	725.20	Espinosa de los Monteros
Bufo spinosus	19/6/2017	tarde	19:02	40	larva	activo	arroyo	VN47	VN4977	1007.87	Lunada
Bufo spinosus	19/6/2017	mediodía	12:27	50	metamórfico	activo	lago o pantano	VN77	VN7576	311.41	Ribota de Ordunte
Bufo spinosus	19/6/2017	mediodía	12:24	100	metamórfico	activo	lago o pantano	VN77	VN7576	308.87	Ribota de Ordunte
Bufo spinosus	19/6/2017	mañana	11:28	100	larva	activo	balsa	VN77	VN7172	394.45	Concejero
Bufo spinosus	19/6/2017	mañana	10:28	250	larva	activo	rio o canal	VN67	VN6373	801.37	Agüera
Bufo spinosus	20/6/2017	noche	01:11	1	adulto	activo	prado o pasto	VN56	VN5766	764.34	Cuestahedo
Bufo spinosus	20/6/2017	noche	00:05	1	adulto	activo	prado o pasto	VN56	VN5368	722.40	Espinosa de los Monteros
Bufo spinosus	23/6/2017	mañana	10:58	1	adulto	inactivo	erial o roca a flor de tierra	VN43	VN4233	1078.97	Huidobro
Bufo spinosus	24/6/2017	mediodía	13:39	36	larva	activo	arroyo	VN47	VN4770	1125.46	Quintanilla del Rebollar
Bufo spinosus	24/6/2017	mediodía	13:37	12	larva	activo	arroyo	VN47	VN4770	1123.15	Quintanilla del Rebollar
Bufo spinosus	24/6/2017	mediodía	13:33	7	larva	activo	arroyo	VN47	VN4770	1121.00	Quintanilla del Rebollar
Bufo spinosus	24/6/2017	mediodía	13:31	21	larva	activo	arroyo	VN47	VN4770	1119.22	Quintanilla del Rebollar
Bufo spinosus	24/6/2017	mediodía	12:23	40	larva	activo	arroyo	VN47	VN4671	1304.70	Espinosa de los Monteros
Bufo spinosus	24/6/2017	mañana	10:16	5	larva	activo	arroyo	VN47	VN4672	1293.54	Espinosa de los Monteros
Bufo spinosus	24/6/2017	mañana	10:16	3	larva	activo	arroyo	VN47	VN4672	1294.95	Espinosa de los Monteros
Bufo spinosus	24/6/2017	mañana	10:15	1	joven	inactivo	prado o pasto	VN47	VN4672	1290.43	Espinosa de los Monteros
Bufo spinosus	24/6/2017	mañana	10:14	1	joven	inactivo	prado o pasto	VN47	VN4672	1291.22	Espinosa de los Monteros
Bufo spinosus	24/6/2017	mañana	10:13	1	joven	inactivo	prado o pasto	VN47	VN4672	1291.60	Espinosa de los Monteros
Bufo spinosus	29/6/2017	tarde	19:13	1	adulto	activo	matorral de montaña	VN47	VN4373	1119.30	Espinosa de los Monteros
Bufo spinosus	10/7/2017	mañana	09:41	1	adulto	inactivo	bosque de ribera	VM58	VM5686	931.99	Ibeas de Juarros
Bufo spinosus	6/4/2019	mediodía	12:18	1	adulto	inactivo	matorral de montaña	VN12	VN1727	933.64	Basconcillos del Tozo
Bufo spinosus	8/4/2019	noche	00:03	1	adulto	activo	cultivo de secano	VN12	VN1428	952.65	Corralejo de Valdelucio
Bufo spinosus	8/4/2019	noche	00:57	1	adulto	activo	robledal marcescente	VN12	VN1125	983.30	Humada
Bufo spinosus	8/4/2019	noche	01:23	1	adulto	activo	robledal marcescente	VN12	VN1125	951.38	Humada
Bufo spinosus	8/4/2019	noche	01:16	1	adulto	activo	robledal marcescente	VN12	VN1125	955.39	Humada
Bufo spinosus	8/4/2019	noche	01:31	1	adulto	activo	charca	VN12	VN1124	945.27	Humada
Bufo spinosus	4/7/2019	mañana	09:18	1	adulto	muerto	arroyo	VN47	VN4573	1004.02	Espinosa de los Monteros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Bufo spinosus	4/7/2019	mañana	11:23	1	joven	inactivo	turbera	VN47	VN4373	1117.82	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mañana	11:18	1	joven	activo	prado o pasto	VN47	VN4373	1117.27	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mañana	11:11	1	joven	inactivo	prado o pasto	VN47	VN4373	1109.18	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mañana	11:09	1	joven	inactivo	prado o pasto	VN47	VN4373	1110.64	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mañana	11:07	1	joven	inactivo	prado o pasto	VN47	VN4373	1113.36	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mañana	11:07	1	joven	activo	prado o pasto	VN47	VN4373	1113.51	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mañana	10:04	1	adulto	inactivo	turbera	VN47	VN4373	1118.95	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mañana	09:57	1	adulto	inactivo	turbera	VN47	VN4373	1120.75	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mediodía	14:12	1	adulto	Atropellado	matorral de montaña	VN47	VN4372	1093.70	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mediodía	13:48	1	adulto	Atropellado	matorral de montaña	VN47	VN4373	1100.07	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mediodía	13:42	1	adulto	Atropellado	matorral de montaña	VN47	VN4373	1078.45	Espinosa de los Monteros
Bufo spinosus	4/7/2019	mediodía	13:42	1	adulto	Atropellado	matorral de montaña	VN47	VN4373	1070.59	Espinosa de los Monteros

Género *Epidalea* Cope, 1864

Epidalea calamita (Laurenti, 1768)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Epidalea calamita	14/7/2016	mediodía	11:00	1000	metamórfico	activo	charca	VM58	VM5987	1010.81	Zalduendo
Epidalea calamita	16/6/2017	mañana	10:21	1	adulto	inactivo	prado o pasto	VN25	VN2557	849.29	Herbosa
Epidalea calamita	20/6/2017	mediodía	13:21	1	joven	muerto	cantera	VM58	VM5788	999.74	Ibeas de Juarros
Epidalea calamita	20/6/2017	mediodía	13:19	1	adulto	muerto	cantera	VM58	VM5788	999.97	Ibeas de Juarros
Epidalea calamita	20/6/2017	mediodía	13:19	1	joven	inactivo	cantera	VM58	VM5788	1000.49	Ibeas de Juarros
Epidalea calamita	20/6/2017	noche	00:51	1	adulto	activo	cultivo de secano	VN55	VN5456	588.95	La Quintana de Rueda
Epidalea calamita	2/7/2017	mañana	10:11	1	adulto	inactivo	cantera	VM58	VM5788	999.88	Ibeas de Juarros
Epidalea calamita	2/7/2017	mañana	08:51	1	joven	inactivo	cantera	VM58	VM5788	1004.08	Ibeas de Juarros
Epidalea calamita	2/7/2017	mañana	10:11	1	joven	inactivo	cantera	VM58	VM5788	1000.16	Ibeas de Juarros
Epidalea calamita	16/7/2017	mediodía	12:15	1	joven	inactivo	cantera	VM58	VM5788	1006.17	Ibeas de Juarros
Epidalea calamita	16/7/2017	mediodía	12:10	1	joven	inactivo	cantera	VM58	VM5788	1005.50	Ibeas de Juarros
Epidalea calamita	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	944.14	Humada
Epidalea calamita	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	943.92	Humada
Epidalea calamita	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	943.84	Humada
Epidalea calamita	8/4/2019	noche	01:28	3	adulto	canto y/o cortejo	charca	VN12	VN1124	943.88	Humada
Epidalea calamita	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	944.20	Humada
Epidalea calamita	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	944.81	Humada
Epidalea calamita	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	945.68	Humada
Epidalea calamita	8/4/2019	madrugada	02:28	1	adulto	activo	prado o pasto	VN23	VN2835	1005.84	Sargentes de la Lora
Epidalea calamita	18/6/2019	mañana	09:09	1	joven	activo	cantera	VM58	VM5788	1005.50	Ibeas de Juarros
Epidalea calamita	19/6/2019	mañana	09:09	1	adulto	inactivo	cantera	VM58	VM5788	1005.41	Ibeas de Juarros
Epidalea calamita	19/6/2019	mañana	09:09	1	adulto	inactivo	cantera	VM58	VM5788	1006.15	Ibeas de Juarros
Epidalea calamita	4/7/2019	tarde	20:26	1	adulto	inactivo	prado o pasto	VN25	VN2657	849.17	Herbosa
Epidalea calamita	4/7/2019	tarde	20:36	2	adulto	inactivo	prado o pasto	VN25	VN2557	849.22	Arnedo
Epidalea calamita	21/6/2019	noche	00:25	1	adulto	activo	cultivo de secano	VN42	VN4524	1001.08	Cernégula

Familia Hylidae Rafinesque, 1814

Género *Hyla* Laurenti, 1768

Hyla molleri (Bedriaga, 1889)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Hyla molleri	14/7/2016	mediodía	11:09	1000	metamórfico	activo	charca	VM58	VM5987	1010.81	Zalduendo
Hyla molleri	18/6/2017	noche	23:52	1	metamórfico	inactivo	bosque de ribera	VN56	VN5668	730.70	Espinosa de los Monteros
Hyla molleri	18/6/2017	noche	23:46	1	metamórfico	activo	bosque de ribera	VN56	VN5668	729.31	Espinosa de los Monteros
Hyla molleri	18/6/2017	noche	23:43	1	metamórfico	activo	bosque de ribera	VN56	VN5668	730.26	Espinosa de los Monteros
Hyla molleri	18/6/2017	noche	23:34	13	larva	activo	balsa	VN56	VN5668	732.65	Espinosa de los Monteros
Hyla molleri	18/6/2017	noche	23:34	200	metamórfico	activo	balsa	VN56	VN5668	732.75	Espinosa de los Monteros
Hyla molleri	20/6/2017	noche	23:18	1	adulto	canto y/o cortejo	bosque de ribera	VN42	VN4821	982.92	Cernégula
Hyla molleri	20/6/2017	noche	23:12	1	adulto	canto y/o cortejo	balsa	VN42	VN4821	982.15	Cernégula
Hyla molleri	20/6/2017	noche	23:08	1	adulto	canto y/o cortejo	balsa	VN42	VN4821	982.11	Cernégula
Hyla molleri	20/6/2017	atardecer	22:03	1	adulto	canto y/o cortejo	lago o pantano	VN42	VN4622	1012.82	Cernégula
Hyla molleri	20/6/2017	atardecer	22:01	1	adulto	canto y/o cortejo	turbera	VN42	VN4622	1013.99	Cernégula
Hyla molleri	24/6/2017	tarde	17:53	1	larva	activo	balsa	VN35	VN3458	824.96	Soncillo
Hyla molleri	24/6/2017	tarde	17:53	1	larva	activo	balsa	VN35	VN3458	824.97	Soncillo
Hyla molleri	24/6/2017	tarde	17:53	1	larva	activo	balsa	VN35	VN3458	824.93	Soncillo
Hyla molleri	24/6/2017	tarde	17:53	1	metamórfico	activo	balsa	VN35	VN3458	824.74	Soncillo
Hyla molleri	24/6/2017	tarde	17:53	1	larva	activo	balsa	VN35	VN3458	824.83	Soncillo
Hyla molleri	24/6/2017	tarde	17:52	1	metamórfico	escape	balsa	VN35	VN3458	824.93	Soncillo
Hyla molleri	25/6/2017	mediodía	13:58	1	larva	activo	balsa	VN42	VN4821	982.11	Cernégula
Hyla molleri	2/7/2017	mañana	08:51	2	adulto	inactivo	cantera	VM58	VM5788	1004.08	Ibeas de Juarros
Hyla molleri	10/7/2017	mañana	11:13	1	joven	muerto	bosque de ribera	VM58	VM5686	931.18	Ibeas de Juarros
Hyla molleri	6/4/2019	mediodía	12:25	1	adulto	activo	matorral de montaña	VN12	VN1727	936.62	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.12	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.40	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.44	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.44	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.80	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.06	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.52	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.01	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.38	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.25	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	909.81	Basconcillos del Tozo
Hyla molleri	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.39	Basconcillos del Tozo
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	arroyo	VN12	VN1124	944.79	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	arroyo	VN12	VN1124	944.50	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	arroyo	VN12	VN1124	944.50	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	arroyo	VN12	VN1124	944.28	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	arroyo	VN12	VN1124	944.30	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	arroyo	VN12	VN1124	944.42	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	arroyo	VN12	VN1124	944.89	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	946.54	Humada

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Hyla molleri	8/4/2019	noche	01:28	1	adulto	canto y/o cortejo	charca	VN12	VN1124	946.04	Humada
Hyla molleri	8/4/2019	noche	01:32	1	adulto	inactivo	charca	VN12	VN1124	943.41	Humada
Hyla molleri	8/4/2019	noche	01:28	1	adulto	inactivo	charca	VN12	VN1124	946.76	Humada
Hyla molleri	8/4/2019	mañana	11:49	1	adulto	inactivo	balsa	VN25	VN2857	909.81	Villamediana de San Román
Hyla molleri	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	825.04	Soncillo
Hyla molleri	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	824.79	Soncillo
Hyla molleri	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	824.64	Soncillo

Familia Ranidae Rafinesque, 1814

Género *Rana* Linnaeus, 1758

Rana dalmatina Bonaparte, 1840

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Rana dalmatina	21/6/2017	tarde	20:02	200	larva	activo	balsa	VN95	VN9854	901.80	Monte Santiago

Rana temporaria Linnaeus, 1758

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Rana temporaria	16/6/2017	tarde	19:06	1	adulto	activo	charca	VN47	VN4272	1197.58	Espinosa de los Monteros
Rana temporaria	16/6/2017	tarde	18:59	5	joven	activo	charca	VN47	VN4272	1197.30	Espinosa de los Monteros
Rana temporaria	16/6/2017	tarde	18:58	4	joven	escape	charca	VN47	VN4272	1197.55	Espinosa de los Monteros
Rana temporaria	16/6/2017	tarde	18:34	1	joven	activo	arroyo	VN47	VN4373	1097.05	Espinosa de los Monteros
Rana temporaria	16/6/2017	tarde	14:22	1	adulto	activo	arroyo	VN47	VN4373	1094.49	Espinosa de los Monteros
Rana temporaria	16/6/2017	tarde	14:05	1	metamórfico	activo	arroyo	VN47	VN4373	1105.24	Espinosa de los Monteros
Rana temporaria	16/6/2017	tarde	14:01	1	adulto	activo	turbera	VN47	VN4373	1112.61	Espinosa de los Monteros
Rana temporaria	16/6/2017	mediodía	12:37	1	adulto	activo	arroyo	VN47	VN4573	1005.47	Espinosa de los Monteros
Rana temporaria	16/6/2017	mediodía	12:34	1	adulto	activo	arroyo	VN47	VN4574	1003.73	Espinosa de los Monteros
Rana temporaria	16/6/2017	mediodía	12:02	30	larva	activo	arroyo	VN47	VN4574	1020.24	Espinosa de los Monteros
Rana temporaria	16/6/2017	mañana	11:32	50	larva	activo	arroyo	VN47	VN4574	1029.66	Espinosa de los Monteros
Rana temporaria	16/6/2017	mañana	11:32	1	adulto	inactivo	arroyo	VN47	VN4574	1028.94	Espinosa de los Monteros
Rana temporaria	16/6/2017	mañana	10:58	9	larva	activo	charca	VN47	VN4574	1004.22	Espinosa de los Monteros
Rana temporaria	19/6/2017	tarde	19:01	1	adulto	escape	arroyo	VN47	VN4977	1008.18	Lunada
Rana temporaria	19/6/2017	tarde	18:08	1	joven	inactivo	balsa	VN47	VN4879	1164.96	Lunada
Rana temporaria	19/6/2017	tarde	17:23	1	adulto	activo	prado o pasto	VN47	VN4679	1330.00	Lunada
Rana temporaria	19/6/2017	tarde	16:58	1	adulto	escape	matorral de montaña	VN47	VN4679	1320.41	Lunada
Rana temporaria	19/6/2017	tarde	16:50	1	adulto	escape	prado o pasto	VN47	VN4679	1320.50	Lunada
Rana temporaria	21/6/2017	tarde	18:41	1	joven	activo	hayedo, robledal o frondosas	WN05	WN0053	847.05	Monte Santiago
Rana temporaria	21/6/2017	tarde	18:37	1	joven	activo	hayedo, robledal o frondosas	WN05	WN0053	841.03	Monte Santiago
Rana temporaria	21/6/2017	tarde	18:33	1	adulto	activo	hayedo, robledal o frondosas	WN05	WN0053	842.04	Monte Santiago
Rana temporaria	21/6/2017	mediodía	13:27	1	adulto	inactivo	rio o canal	VN95	VN9954	839.63	Monte Santiago
Rana temporaria	24/6/2017	mediodía	12:24	1	adulto	escape	turbera	VN47	VN4671	1303.46	Espinosa de los Monteros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Rana temporaria	24/6/2017	mediodía	12:22	1	adulto	muerto	arroyo	VN47	VN4671	1308.72	Espinosa de los Monteros
Rana temporaria	24/6/2017	mañana	10:25	1	joven	escape	turbera	VN47	VN4671	1313.58	Espinosa de los Monteros
Rana temporaria	24/6/2017	mañana	10:23	1	adulto	activo	turbera	VN47	VN4671	1314.02	Espinosa de los Monteros
Rana temporaria	24/6/2017	mañana	10:13	1	adulto	activo	prado o pasto	VN47	VN4672	1292.30	Espinosa de los Monteros
Rana temporaria	29/6/2017	tarde	19:11	1	adulto	activo	arroyo	VN47	VN4373	1119.79	Espinosa de los Monteros
Rana temporaria	4/7/2019	mañana	09:11	1000	larva	activo	arroyo	VN47	VN4573	1008.37	Espinosa de los Monteros
Rana temporaria	4/7/2019	mañana	10:41	1	adulto	activo	turbera	VN47	VN4373	1117.86	Espinosa de los Monteros
Rana temporaria	4/7/2019	mañana	10:34	1	adulto	activo	turbera	VN47	VN4373	1122.98	Espinosa de los Monteros
Rana temporaria	4/7/2019	mañana	09:55	1	joven	activo	turbera	VN47	VN4373	1121.02	Espinosa de los Monteros
Rana temporaria	4/7/2019	mañana	10:18	1	adulto	activo	turbera	VN47	VN4373	1125.41	Espinosa de los Monteros
Rana temporaria	4/7/2019	tarde	13:50	17	metamórfico	activo	arroyo	VN47	VN4372	1096.17	Espinosa de los Monteros
Rana temporaria	4/7/2019	tarde	13:50	200	larva	activo	arroyo	VN47	VN4372	1096.17	Espinosa de los Monteros

Género *Pelophylax* Fitzinger, 1843

Pelophylax perezi (Seoane, 1885)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Pelophylax perezi	9/7/2016	mañana	10:30	1	adulto	escape	balsa	VN42	VN4622	1012.42	Cernégula
Pelophylax perezi	9/7/2016	mañana	10:10	30	adulto	escape	balsa	VN42	VN4820	981.34	Cernégula
Pelophylax perezi	9/7/2016	mañana	10:10	200	joven	escape	balsa	VN42	VN4820	981.34	Cernégula
Pelophylax perezi	14/7/2016	mediodía	11:11	500	metamórfico	activo	charca	VM58	VM5987	1010.81	Zalduendo
Pelophylax perezi	16/7/2016	tarde	19:34	8	adulto	activo	arroyo	VM68	VM6186	972.78	Arlanzón.
Pelophylax perezi	22/7/2016	tarde	18:25	1	adulto	activo	hayedo, robledal o frondosas	VM88	VM8584	1056.98	Pradoluengo
Pelophylax perezi	16/6/2017	noche	00:32	4	adulto	canto y/o cortejo	rio o canal	VN56	VN5469	742.83	Espinosa de los Monteros
Pelophylax perezi	16/6/2017	noche	00:17	1	adulto	inactivo	rio o canal	VN56	VN5469	747.94	Espinosa de los Monteros
Pelophylax perezi	16/6/2017	noche	00:15	2	adulto	canto y/o cortejo	rio o canal	VN56	VN5469	747.21	Espinosa de los Monteros
Pelophylax perezi	16/6/2017	noche	00:10	7	adulto	canto y/o cortejo	rio o canal	VN56	VN5469	744.93	Espinosa de los Monteros
Pelophylax perezi	17/6/2017	mediodía	12:06	1	adulto	escape	balsa	VN87	VN8577	239.47	Orrantia, Ayega
Pelophylax perezi	17/6/2017	mediodía	12:04	3	larva	activo	balsa	VN87	VN8577	239.36	Orrantia, Ayega
Pelophylax perezi	17/6/2017	mediodía	12:04	1	adulto	activo	balsa	VN87	VN8577	239.53	Orrantia, Ayega
Pelophylax perezi	17/6/2017	mañana	11:57	2	adulto	escape	balsa	VN87	VN8577	238.96	Orrantia, Ayega
Pelophylax perezi	17/6/2017	mañana	11:57	10	larva	activo	balsa	VN87	VN8577	238.89	Orrantia, Ayega
Pelophylax perezi	17/6/2017	mañana	10:50	1	adulto	inactivo	bosque de ribera	VN87	VN8176	324.34	Opio, Valle de Mena.
Pelophylax perezi	18/6/2017	tarde	15:50	1	adulto	activo	rio o canal	VN46	VN4666	718.90	Quisicedo
Pelophylax perezi	18/6/2017	mañana	10:58	3	adulto	activo	lago o pantano	VN46	VN4864	643.81	Cornejo.
Pelophylax perezi	18/6/2017	mañana	10:49	2	adulto	activo	lago o pantano	VN46	VN4864	644.00	Cornejo.
Pelophylax perezi	18/6/2017	mañana	10:01	3	joven	escape	lago o pantano	VN56	VN5761	656.10	Gayangos.
Pelophylax perezi	18/6/2017	mañana	09:58	12	adulto	canto y/o cortejo	lago o pantano	VN56	VN5861	653.58	Gayangos.
Pelophylax perezi	19/6/2017	mañana	10:59	1	joven	escape	arroyo	VN76	VN7269	373.39	Lezana de Mena
Pelophylax perezi	19/6/2017	mañana	10:56	1	adulto	activo	arroyo	VN76	VN7269	373.36	Lezana de Mena
Pelophylax perezi	19/6/2017	mañana	10:42	1	adulto	canto y/o cortejo	rio o canal	VN67	VN6272	777.20	Agüera
Pelophylax perezi	19/6/2017	mañana	10:29	3	adulto	escape	rio o canal	VN67	VN6373	801.52	Agüera
Pelophylax perezi	19/6/2017	mañana	10:26	4	adulto	escape	rio o canal	VN67	VN6373	805.33	Agüera

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Pelophylax perezi	19/6/2017	mañana	10:24	8	adulto	canto y/o cortejo	rio o canal	VN67	VN6373	805.93	Agüera
Pelophylax perezi	19/6/2017	mañana	10:24	3	adulto	activo	rio o canal	VN67	VN6373	806.18	Agüera
Pelophylax perezi	20/6/2017	noche	22:57	39	adulto	canto y/o cortejo	balsa	VN42	VN4821	982.01	Cernégula
Pelophylax perezi	20/6/2017	noche	22:43	44	adulto	canto y/o cortejo	lago o pantano	VN42	VN4820	981.38	Cernégula
Pelophylax perezi	20/6/2017	noche	22:43	43	adulto	activo	lago o pantano	VN42	VN4820	982.05	Cernégula
Pelophylax perezi	20/6/2017	atardecer	22:11	7	adulto	canto y/o cortejo	lago o pantano	VN42	VN4622	1012.51	Cernégula
Pelophylax perezi	20/6/2017	noche	01:16	1	adulto	canto y/o cortejo	rio o canal	VN56	VN5667	724.22	Espinosa de los Monteros
Pelophylax perezi	21/6/2017	tarde	19:43	1	adulto	canto y/o cortejo	balsa	VN95	VN9854	901.74	Monte Santiago
Pelophylax perezi	21/6/2017	mediodía	12:33	27	adulto	canto y/o cortejo	rio o canal	VN95	VN9954	836.53	Monte Santiago
Pelophylax perezi	21/6/2017	noche	00:01	5	adulto	escape	prado o pasto	VN42	VN4820	982.28	Cernégula
Pelophylax perezi	22/6/2017	tarde	18:37	2	adulto	canto y/o cortejo	lago o pantano	VM59	VM5892	934.54	Atapuerca
Pelophylax perezi	23/6/2017	tarde	17:55	1	adulto	escape	balsa	VN35	VN3458	824.95	Soncillo
Pelophylax perezi	24/6/2017	tarde	19:31	1	adulto	activo	rio o canal	VN46	VN4067	852.03	Túnel de La Engaña
Pelophylax perezi	24/6/2017	tarde	19:17	1	joven	escape	rio o canal	VN46	VN4066	767.83	Túnel de La Engaña
Pelophylax perezi	24/6/2017	tarde	19:17	1	adulto	activo	rio o canal	VN46	VN4066	772.51	Túnel de La Engaña
Pelophylax perezi	24/6/2017	tarde	19:16	1	joven	activo	rio o canal	VN46	VN4066	773.26	Túnel de La Engaña
Pelophylax perezi	24/6/2017	tarde	19:16	1	adulto	activo	rio o canal	VN46	VN4066	774.24	Túnel de La Engaña
Pelophylax perezi	24/6/2017	tarde	19:14	1	adulto	escape	rio o canal	VN46	VN4066	776.96	Túnel de La Engaña
Pelophylax perezi	24/6/2017	tarde	19:11	1	adulto	activo	rio o canal	VN46	VN4067	800.57	Túnel de La Engaña
Pelophylax perezi	24/6/2017	tarde	18:53	100	larva	activo	charca	VN46	VN4066	766.19	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:53	1	joven	escape	charca	VN46	VN4066	765.93	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:53	1	adulto	activo	charca	VN46	VN4066	765.05	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:52	1	joven	escape	charca	VN46	VN4066	764.20	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:51	1	joven	escape	charca	VN46	VN4066	764.36	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:51	1	adulto	activo	charca	VN46	VN4066	764.47	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:50	1	adulto	activo	charca	VN46	VN4066	764.55	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:49	1	joven	escape	charca	VN46	VN4066	764.53	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:49	1	adulto	activo	charca	VN46	VN4066	764.82	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:48	1	adulto	activo	charca	VN46	VN4066	764.81	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:48	1	joven	escape	charca	VN46	VN4066	764.74	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:48	200	larva	activo	charca	VN46	VN4066	765.10	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:47	1	adulto	activo	charca	VN46	VN4066	760.87	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:21	1	adulto	activo	charca	VN46	VN4066	760.54	La Engaña
Pelophylax perezi	24/6/2017	tarde	18:21	1	adulto	escape	charca	VN46	VN4066	760.55	La Engaña
Pelophylax perezi	24/6/2017	tarde	17:53	1	larva	activo	balsa	VN35	VN3458	824.99	Soncillo
Pelophylax perezi	24/6/2017	tarde	17:52	1	larva	activo	balsa	VN35	VN3458	824.92	Soncillo
Pelophylax perezi	25/6/2017	tarde	14:01	1	larva	activo	balsa	VN42	VN4821	982.17	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:44	1	joven	escape	balsa	VN42	VN4821	982.67	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:44	1	joven	escape	balsa	VN42	VN4821	982.76	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:44	1	joven	activo	balsa	VN42	VN4821	982.54	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:44	1	adulto	activo	balsa	VN42	VN4821	982.62	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:43	1	joven	activo	balsa	VN42	VN4821	982.65	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:43	1	adulto	escape	balsa	VN42	VN4821	982.63	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:47	1	adulto	activo	balsa	VN42	VN4821	982.11	Cernégula
Pelophylax perezi	25/6/2017	mediodía	12:46	1	adulto	activo	balsa	VN42	VN4820	982.23	Cernégula

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Pelophylax perezi	25/6/2017	mediodía	12:46	1	adulto	inactivo	balsa	VN42	VN4820	982.12	Cernégula
Pelophylax perezi	27/6/2017	tarde	16:52	1	joven	escape	balsa	VN43	VN4033	1007.26	Nocedo
Pelophylax perezi	27/6/2017	tarde	16:52	1	adulto	escape	balsa	VN43	VN4033	1007.23	Nocedo
Pelophylax perezi	27/6/2017	tarde	15:31	1	adulto	escape	balsa	VN43	VN4033	1007.21	Nocedo
Pelophylax perezi	27/6/2017	tarde	15:29	1	adulto	escape	balsa	VN43	VN4033	1007.25	Nocedo
Pelophylax perezi	27/6/2017	tarde	15:29	1	joven	escape	balsa	VN43	VN4033	1007.26	Nocedo
Pelophylax perezi	27/6/2017	mañana	11:25	1	adulto	canto y/o cortejo	rio o canal	VN33	VN3433	683.03	San Felices del Rudrón
Pelophylax perezi	27/6/2017	mañana	09:53	1	adulto	canto y/o cortejo	rio o canal	VN33	VN3431	698.05	Covanera
Pelophylax perezi	28/6/2017	tarde	20:29	1	adulto	amplexo	lago o pantano	VN12	VN1827	914.57	Basconcillos del Tozo
Pelophylax perezi	28/6/2017	tarde	20:29	1	adulto	amplexo	lago o pantano	VN12	VN1827	914.55	Basconcillos del Tozo
Pelophylax perezi	28/6/2017	noche	22:37	1	adulto	activo	turbera	VN12	VN1921	1018.34	Fuencaliente de Puerta
Pelophylax perezi	28/6/2017	atardecer	21:48	1	joven	escape	arroyo	VN22	VN2022	998.88	Talamillo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:43	1	joven	escape	arroyo	VN22	VN2022	998.42	Talamillo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:43	1	joven	escape	arroyo	VN22	VN2022	998.30	Talamillo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:43	1	joven	activo	arroyo	VN22	VN2022	998.24	Talamillo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:31	1	joven	escape	balsa	VN22	VN2122	984.73	Talamillo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:31	1	adulto	activo	balsa	VN22	VN2122	984.65	Talamillo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:29	1	adulto	activo	balsa	VN22	VN2122	984.66	Talamillo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:18	1	joven	activo	arroyo	VN22	VN2325	986.34	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:18	1	adulto	escape	arroyo	VN22	VN2325	986.23	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:17	1	joven	escape	arroyo	VN22	VN2325	986.17	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:17	1	adulto	escape	arroyo	VN22	VN2325	986.17	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:17	1	joven	escape	arroyo	VN22	VN2325	986.08	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:16	1	joven	escape	arroyo	VN22	VN2325	985.99	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:09	1	joven	activo	balsa	VN22	VN2326	984.32	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:09	1	joven	activo	balsa	VN22	VN2326	984.24	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:09	1	adulto	escape	balsa	VN22	VN2326	984.27	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:08	1	adulto	escape	balsa	VN22	VN2326	984.14	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:08	1	joven	escape	balsa	VN22	VN2326	984.17	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:07	1	adulto	activo	balsa	VN22	VN2326	984.04	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:06	1	joven	activo	balsa	VN22	VN2326	983.98	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:06	1	adulto	escape	balsa	VN22	VN2326	983.89	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:06	1	adulto	escape	balsa	VN22	VN2326	983.89	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:05	1	adulto	activo	balsa	VN22	VN2326	983.79	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:05	1	joven	activo	balsa	VN22	VN2326	983.75	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:05	1	adulto	activo	balsa	VN22	VN2326	983.70	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:05	1	adulto	escape	balsa	VN22	VN2326	983.63	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:02	1	joven	activo	balsa	VN22	VN2326	983.31	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:02	1	joven	activo	balsa	VN22	VN2326	983.15	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:01	1	adulto	escape	balsa	VN22	VN2326	983.11	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:01	1	joven	escape	balsa	VN22	VN2326	983.08	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:01	1	adulto	escape	balsa	VN22	VN2326	983.05	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	atardecer	21:03	1	adulto	escape	balsa	VN22	VN2326	983.05	Trashaedo del Tozo
Pelophylax perezi	28/6/2017	tarde	20:56	1	joven	escape	charca	VN22	VN2225	946.65	Basconcillos del Tozo
Pelophylax perezi	28/6/2017	tarde	20:54	1	adulto	inactivo	charca	VN22	VN2225	946.58	Basconcillos del Tozo

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Pelophylax perezi	28/6/2017	tarde	20:11	29	adulto	activo	lago o pantano	VN12	VN1827	914.34	Basconcillos del Tozo
Pelophylax perezi	28/6/2017	tarde	20:13	1	adulto	canto y/o cortejo	lago o pantano	VN12	VN1827	914.30	Basconcillos del Tozo
Pelophylax perezi	28/6/2017	tarde	20:11	1	adulto	canto y/o cortejo	lago o pantano	VN12	VN1827	914.58	Basconcillos del Tozo
Pelophylax perezi	28/6/2017	tarde	19:33	1	adulto	activo	balsa	VN23	VN2433	1004.02	Valdeajos, Sargentes de la Lora
Pelophylax perezi	28/6/2017	tarde	18:18	1	larva	activo	balsa	VN23	VN2833	1009.74	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:31	1	joven	activo	balsa	VN23	VN2833	1008.98	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:31	1	adulto	escape	balsa	VN23	VN2833	1008.96	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:30	1	joven	escape	balsa	VN23	VN2833	1008.93	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:28	1	adulto	escape	balsa	VN23	VN2833	1008.95	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:28	1	joven	escape	balsa	VN23	VN2833	1008.90	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:25	1	adulto	activo	balsa	VN23	VN2833	1008.92	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:23	1	joven	escape	balsa	VN23	VN2833	1009.09	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:22	1	adulto	escape	balsa	VN23	VN2833	1009.23	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:21	1	adulto	inactivo	balsa	VN23	VN2833	1009.29	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:18	1	adulto	escape	balsa	VN23	VN2833	1009.48	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:18	1	joven	activo	balsa	VN23	VN2833	1009.58	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:14	1	joven	escape	balsa	VN23	VN2833	1009.67	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:14	1	joven	activo	balsa	VN23	VN2833	1009.55	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:13	1	joven	escape	balsa	VN23	VN2833	1009.45	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:13	1	adulto	escape	balsa	VN23	VN2833	1009.47	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:13	1	adulto	activo	balsa	VN23	VN2833	1009.46	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:11	1	joven	escape	balsa	VN23	VN2833	1009.32	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:09	1	adulto	activo	balsa	VN23	VN2833	1009.25	Ayoluengo
Pelophylax perezi	28/6/2017	tarde	18:09	1	adulto	canto y/o cortejo	balsa	VN23	VN2833	1009.15	Ayoluengo
Pelophylax perezi	27/7/2017	tarde	15:31	1	adulto	activo	balsa	VN43	VN4033	1007.21	Nocedo
Pelophylax perezi	27/7/2017	tarde	15:25	1	adulto	escape	balsa	VN43	VN4033	1007.18	Nocedo
Pelophylax perezi	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.26	Basconcillos del Tozo
Pelophylax perezi	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.06	Basconcillos del Tozo
Pelophylax perezi	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.39	Basconcillos del Tozo
Pelophylax perezi	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	910.22	Basconcillos del Tozo
Pelophylax perezi	6/4/2019	mediodía	12:31	1	adulto	canto y/o cortejo	rio o canal	VN12	VN1827	909.85	Basconcillos del Tozo
Pelophylax perezi	8/4/2019	mediodía	12:12	1	adulto	activo	balsa	VN25	VN2758	897.64	Villamediana de San Román
Pelophylax perezi	19/6/2019	mañana	09:09	1	joven	inactivo	cantera	VM58	VM5788	1004.38	Ibeas de Juarros
Pelophylax perezi	4/7/2019	atardecer	21:04	1	joven	canto y/o cortejo	lago o pantano	VN25	VN2657	845.19	Arnedo
Pelophylax perezi	4/7/2019	atardecer	21:11	1	adulto	canto y/o cortejo	lago o pantano	VN25	VN2657	846.00	Arnedo
Pelophylax perezi	4/7/2019	atardecer	21:11	1	adulto	canto y/o cortejo	lago o pantano	VN25	VN2557	845.61	Arnedo
Pelophylax perezi	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	824.96	Soncillo
Pelophylax perezi	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	824.96	Soncillo
Pelophylax perezi	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	824.99	Soncillo
Pelophylax perezi	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	825.00	Soncillo
Pelophylax perezi	4/7/2019	noche	22:41	1	adulto	canto y/o cortejo	charca	VN35	VN3458	825.03	Soncillo

Chelonii Latreille 1800

Familia Emydidae Rafinesque, 1815

Género *Trachemys* Agassiz, 1857

Trachemys scripta (Thunberg, 1792)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Trachemys scripta	27/6/2017	mañana	10:01	1	Adulto	activo	rio o canal	VN33	VN3431	697.44	Covanera

Familia Geoemydidae Theobald, 1868

Género *Mauremys* Gray, 1869

Mauremys leprosa (Schweigger, 1812)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Mauremys leprosa	16/6/2017	mañana	10:34	1	adulto	inactivo	lago o pantano	VN25	VN2557	845.91	Herbosa
Mauremys leprosa	27/6/2017	mediodía	12:27	1	adulto	activo	rio o canal	VN33	VN3739	661.53	Quintanilla-Escalada
Mauremys leprosa	4/7/2019	atardecer	21:01	1	adulto	activo	lago o pantano	VN25	VN2557	845.77	Arnedo

Squamata Oppel, 1811

Familia Anguidae Oppel, 1811

Género *Anguis* Linnaeus, 1758

Anguis fragilis Linnaeus, 1758

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Anguis fragilis	17/7/2016	mañana	09:30	1	adulto	activo	bosque de ribera	VM58	VM5686	931.15	Ibeas de Juarros
Anguis fragilis	16/6/2017	tarde	19:28	1	adulto	escape	prado o pasto	VN47	VN4674	982.60	Espinosa de los Monteros
Anguis fragilis	16/6/2017	tarde	19:26	1	adulto	activo	prado o pasto	VN47	VN4674	982.35	Espinosa de los Monteros
Anguis fragilis	17/6/2017	mañana	08:55	1	adulto	inactivo	prado o pasto	VN87	VN8179	191.83	Santecilla
Anguis fragilis	18/6/2017	atardecer	20:50	1	adulto	inactivo	matorral de montaña	VN36	VN3663	730.74	Cidad de Valdeporres
Anguis fragilis	18/6/2017	tarde	18:30	1	adulto	inactivo	matorral de montaña	VN36	VN3664	708.39	Busnela
Anguis fragilis	18/6/2017	tarde	17:54	1	adulto	inactivo	matorral de montaña	VN36	VN3664	707.30	Busnela
Anguis fragilis	19/6/2017	mañana	11:12	1	adulto	inactivo	prado o pasto	VN76	VN7169	379.41	Lezana de Mena
Anguis fragilis	27/6/2017	tarde	16:08	1	adulto	inactivo	prado o pasto	VN43	VN4033	1007.23	Nocedo
Anguis fragilis	9/7/2017	mañana	10:10	1	adulto	activo	bosque de ribera	VM58	VM5686	931.12	Ibeas de Juarros
Anguis fragilis	21/7/2017	mañana	09:19	1	adulto	activo	bosque de ribera	VM58	VM5686	931.47	Ibeas de Juarros
Anguis fragilis	6/4/2019	tarde	14:14	1	adulto	Atropellado	hayedo, robledal o frondosas	VN33	VN3134	937.96	Sargentes de la Lora
Anguis fragilis	3/7/2019	tarde	19:56	1	adulto	inactivo	prado o pasto	VN56	VN5768	718.99	Espinosa de los Monteros
Anguis fragilis	3/7/2019	atardecer	20:55	1	adulto	inactivo	prado o pasto	VN56	VN5768	711.10	Espinosa de los Monteros
Anguis fragilis	3/7/2019	atardecer	21:25	1	adulto	inactivo	prado o pasto	VN56	VN5768	713.32	Espinosa de los Monteros
Anguis fragilis	3/7/2019	atardecer	21:25	1	joven	inactivo	prado o pasto	VN56	VN5768	713.38	Espinosa de los Monteros
Anguis fragilis	3/7/2019	atardecer	21:25	1	joven	inactivo	prado o pasto	VN56	VN5768	713.00	Espinosa de los Monteros
Anguis fragilis	3/7/2019	atardecer	21:25	1	joven	inactivo	prado o pasto	VN56	VN5768	713.15	Espinosa de los Monteros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Anguis fragilis	3/7/2019	atardecer	21:25	1	adulto	inactivo	prado o pasto	VN56	VN5768	713.15	Espinosa de los Monteros
Anguis fragilis	3/7/2019	atardecer	21:33	1	joven	inactivo	prado o pasto	VN56	VN5768	711.98	Espinosa de los Monteros
Anguis fragilis	4/7/2019	tarde	15:03	1	adulto	inactivo	prado o pasto	VN47	VN4674	981.89	Espinosa de los Monteros
Anguis fragilis	4/7/2019	tarde	20:14	1	adulto	inactivo	prado o pasto	VN25	VN2657	861.69	Herbosa

Familia Scincidae Oppel, 1811

Género *Chalcides* Laurenti, 1768

Chalcides striatus (Cuvier, 1829)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Chalcides striatus	9/7/2016	mañana	10:53	2	adulto	termorregulación	prado o pasto	VN42	VN4723	1014.94	Cernégula
Chalcides striatus	9/7/2016	mañana	10:24	1	adulto	termorregulación	cultivo de secano	VN42	VN4721	987.78	Cernégula
Chalcides striatus	21/7/2016	tarde	18:55	1	adulto	inactivo	prado o pasto	VN40	VN4406	1005.75	Gredilla la Polera
Chalcides striatus	21/7/2016	tarde	18:55	1	adulto	inactivo	prado o pasto	VN40	VN4406	1005.75	Gredilla la Polera
Chalcides striatus	22/7/2016	atardecer	20:42	3	adulto	inactivo	matorral de montaña	VN33	VN3434	819.96	San Felices del Rudrón
Chalcides striatus	20/6/2017	tarde	20:03	1	adulto	inactivo	prado o pasto	VN40	VN4304	984.09	Ubierna
Chalcides striatus	20/6/2017	tarde	19:53	1	joven	inactivo	prado o pasto	VN40	VN4304	986.75	Ubierna
Chalcides striatus	20/6/2017	tarde	19:41	1	adulto	inactivo	prado o pasto	VN40	VN4304	988.24	Ubierna
Chalcides striatus	22/6/2017	tarde	20:56	1	adulto	escape	prado o pasto	VN40	VN4306	1011.28	Gredilla la Polera
Chalcides striatus	22/6/2017	tarde	20:53	1	adulto	activo	prado o pasto	VN40	VN4306	1009.16	Gredilla la Polera
Chalcides striatus	22/6/2017	tarde	20:52	1	adulto	activo	prado o pasto	VN40	VN4306	1008.35	Gredilla la Polera
Chalcides striatus	22/6/2017	tarde	20:52	1	adulto	inactivo	prado o pasto	VN40	VN4306	1008.18	Gredilla la Polera
Chalcides striatus	22/6/2017	tarde	20:49	1	adulto	escape	prado o pasto	VN40	VN4306	1009.34	Gredilla la Polera
Chalcides striatus	22/6/2017	tarde	20:48	1	adulto	escape	prado o pasto	VN40	VN4306	1010.08	Gredilla la Polera
Chalcides striatus	22/6/2017	tarde	20:39	1	adulto	activo	prado o pasto	VN40	VN4306	1008.62	Gredilla la Polera
Chalcides striatus	22/6/2017	mañana	10:10	1	adulto	escape	turbera	VN22	VN2027	924.51	Basconcillos del Tozo
Chalcides striatus	22/6/2017	mañana	10:03	1	adulto	escape	prado o pasto	VN22	VN2027	926.03	Basconcillos del Tozo
Chalcides striatus	23/6/2017	mañana	09:57	1	adulto	activo	matorral mediterráneo	VN33	VN3530	748.37	Tubilla del Agua
Chalcides striatus	23/6/2017	mañana	09:43	1	adulto	activo	prado o pasto	VN33	VN3531	738.38	Tubilla del Agua
Chalcides striatus	23/6/2017	mañana	09:39	1	adulto	escape	prado o pasto	VN33	VN3531	727.06	Tubilla del Agua
Chalcides striatus	24/6/2017	tarde	20:54	1	joven	activo	cultivo de secano	VN46	VN4762	783.20	Merindad de Sotocueva
Chalcides striatus	24/6/2017	tarde	20:51	1	joven	inactivo	encinar, alcornocal o dehesa	VN46	VN4762	789.49	Merindad de Sotocueva
Chalcides striatus	24/6/2017	tarde	20:37	1	adulto	inactivo	encinar, alcornocal o dehesa	VN46	VN4762	788.03	Merindad de Sotocueva
Chalcides striatus	25/6/2017	tarde	20:25	1	adulto	escape	prado o pasto	VN40	VN4305	1007.48	Ubierna
Chalcides striatus	25/6/2017	tarde	20:19	1	adulto	inactivo	prado o pasto	VN40	VN4305	1008.73	Ubierna
Chalcides striatus	25/6/2017	tarde	17:59	1	adulto	inactivo	prado o pasto	VM58	VM5888	1023.04	Zalduendo
Chalcides striatus	25/6/2017	tarde	17:59	1	adulto	inactivo	prado o pasto	VM58	VM5888	1023.04	Zalduendo
Chalcides striatus	25/6/2017	tarde	17:18	1	adulto	activo	prado o pasto	VM58	VM5888	1018.30	Zalduendo
Chalcides striatus	25/6/2017	mañana	11:46	1	joven	activo	prado o pasto	VN40	VN4406	997.26	Gredilla la Polera
Chalcides striatus	25/6/2017	mañana	10:30	1	adulto	activo	prado o pasto	VN40	VN4405	982.83	Gredilla la Polera
Chalcides striatus	25/6/2017	mañana	10:23	1	joven	activo	encinar, alcornocal o dehesa	VN40	VN4405	965.50	Gredilla la Polera
Chalcides striatus	25/6/2017	mañana	09:52	1	adulto	activo	prado o pasto	VN40	VN4405	972.91	Gredilla la Polera

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Chalcides striatus	27/6/2017	tarde	16:33	1	adulto	activo	prado o pasto	VN43	VN4033	1059.82	Nocedo
Chalcides striatus	6/4/2019	mediodía	12:43	1	adulto	termorregulación	robledal marcescente	VN12	VN1827	916.20	Basconcillos del Tozo
Chalcides striatus	6/4/2019	tarde	14:01	1	adulto	inactivo	prado o pasto	VN23	VN2835	1007.75	Sargentes de la Lora
Chalcides striatus	5/7/2019	tarde	19:58	1	adulto	escape	prado o pasto	VN43	VN4234	1095.76	Huidobro
Chalcides striatus	5/7/2019	tarde	19:41	1	adulto	activo	prado o pasto	VN43	VN4333	1088.59	Huidobro
Chalcides striatus	5/7/2019	tarde	19:26	1	adulto	activo	prado o pasto	VN43	VN4333	1079.56	Huidobro
Chalcides striatus	5/7/2019	tarde	19:19	1	adulto	activo	prado o pasto	VN43	VN4333	1095.34	Huidobro
Chalcides striatus	5/7/2019	tarde	19:08	1	adulto	activo	prado o pasto	VN43	VN4233	1082.56	Huidobro
Chalcides striatus	5/7/2019	tarde	19:03	1	adulto	activo	prado o pasto	VN43	VN4233	1090.33	Huidobro

Familia Lacertidae Oppel, 1811

Género *Lacerta* Linnaeus, 1758

Lacerta bilineata (Daudin, 1802)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Lacerta bilineata	2/7/2016	mañana	11:20	1	adulto	activo	prado o pasto	VM58	VM5686	930.27	Ibeas de Juarros
Lacerta bilineata	2/7/2016	mañana	11:06	1	adulto	termorregulación	prado o pasto	VM58	VM5686	930.84	Ibeas de Juarros
Lacerta bilineata	9/7/2016	mañana	10:44	1	adulto	escape	prado o pasto	VN42	VN4623	1016.21	Cernégula
Lacerta bilineata	9/7/2016	mañana	10:32	6	adulto	escape	turbera	VN42	VN4622	1013.79	Cernégula
Lacerta bilineata	13/7/2016	tarde	19:13	2	adulto	inactivo	prado o pasto	VM59	VM5892	936.26	Atapuerca
Lacerta bilineata	16/7/2016	mañana	09:30	16	adulto	activo	prado o pasto	VM58	VM5686	930.81	Ibeas de Juarros
Lacerta bilineata	16/6/2017	tarde	19:26	1	adulto	inactivo	prado o pasto	VN47	VN4674	982.60	Espinosa de los Monteros
Lacerta bilineata	16/6/2017	tarde	19:26	1	adulto	muerto	prado o pasto	VN47	VN4674	982.41	Espinosa de los Monteros
Lacerta bilineata	16/6/2017	mañana	11:11	1	adulto	muerto	matorral de montaña	VN47	VN4574	1004.22	Espinosa de los Monteros
Lacerta bilineata	17/6/2017	mediodía	13:11	2	adulto	escape	prado o pasto	VN87	VN8478	279.82	Antuñano, Bortedo
Lacerta bilineata	18/6/2017	tarde	19:35	1	adulto	escape	matorral de montaña	VN36	VN3664	807.09	Busnela
Lacerta bilineata	18/6/2017	tarde	18:28	1	adulto	escape	matorral de montaña	VN36	VN3664	708.26	Busnela
Lacerta bilineata	18/6/2017	tarde	18:08	1	adulto	escape	matorral de montaña	VN36	VN3664	707.87	Busnela
Lacerta bilineata	18/6/2017	tarde	17:16	1	adulto	activo	matorral de montaña	VN36	VN3664	707.66	Busnela
Lacerta bilineata	18/6/2017	tarde	17:13	1	adulto	escape	matorral de montaña	VN36	VN3664	707.21	Busnela
Lacerta bilineata	18/6/2017	tarde	17:10	1	adulto	activo	matorral de montaña	VN36	VN3664	707.83	Busnela
Lacerta bilineata	18/6/2017	tarde	17:09	1	adulto	escape	matorral de montaña	VN36	VN3664	707.35	Busnela
Lacerta bilineata	18/6/2017	tarde	15:52	1	adulto	escape	prado o pasto	VN46	VN4666	715.06	Quisicedo
Lacerta bilineata	19/6/2017	mañana	10:42	1	adulto	activo	prado o pasto	VN67	VN6272	787.34	Agüera
Lacerta bilineata	22/6/2017	tarde	18:28	1	adulto	escape	prado o pasto	VM59	VM5892	938.44	Atapuerca
Lacerta bilineata	22/6/2017	tarde	17:50	1	adulto	activo	bosque de ribera	VM58	VM5686	931.42	Ibeas de Juarros
Lacerta bilineata	27/6/2017	tarde	15:56	1	adulto	activo	prado o pasto	VN43	VN4133	1004.36	Nocedo
Lacerta bilineata	4/7/2017	mediodía	12:04	1	adulto	activo	bosque de ribera	VM58	VM5686	931.26	Ibeas de Juarros
Lacerta bilineata	4/7/2017	mediodía	12:04	1	adulto	termorregulación	bosque de ribera	VM58	VM5686	931.19	Ibeas de Juarros
Lacerta bilineata	17/7/2017	mediodía	11:36	1	adulto	escape	prado o pasto	VM58	VM5686	930.93	Ibeas de Juarros
Lacerta bilineata	17/7/2017	mediodía	11:43	1	adulto	activo	prado o pasto	VM58	VM5686	931.07	Ibeas de Juarros
Lacerta bilineata	19/7/2017	mañana	09:59	1	adulto	activo	prado o pasto	VM58	VM5686	930.99	Ibeas de Juarros
Lacerta bilineata	21/7/2017	mañana	11:04	1	adulto	escape	bosque de ribera	VM58	VM5686	930.58	Ibeas de Juarros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Lacerta bilineata	6/4/2019	mañana	11:08	1	adulto	activo	prado o pasto	VN12	VN1828	905.12	Basconcillos del Tozo
Lacerta bilineata	6/4/2019	mañana	11:17	1	adulto	activo	matorral de montaña	VN12	VN1828	905.26	Basconcillos del Tozo
Lacerta bilineata	6/4/2019	mañana	11:42	1	adulto	activo	prado o pasto	VN12	VN1828	910.52	Basconcillos del Tozo
Lacerta bilineata	6/4/2019	tarde	17:18	1	adulto	activo	matorral de montaña	VN25	VN2658	892.37	Herbosa
Lacerta bilineata	6/4/2019	tarde	17:16	1	adulto	activo	matorral de montaña	VN25	VN2658	892.02	Herbosa
Lacerta bilineata	8/4/2019	tarde	15:01	1	adulto	escape	matorral de montaña	VN45	VN4058	706.12	Quintanabaldo
Lacerta bilineata	8/4/2019	tarde	15:01	1	adulto	activo	matorral de montaña	VN45	VN4058	704.90	Quintanabaldo
Lacerta bilineata	8/4/2019	tarde	14:13	1	adulto	escape	matorral de montaña	VN45	VN4058	683.24	Quintanabaldo
Lacerta bilineata	8/4/2019	tarde	14:08	1	adulto	escape	matorral de montaña	VN45	VN4058	684.16	Quintanabaldo
Lacerta bilineata	8/4/2019	tarde	14:02	1	adulto	activo	matorral de montaña	VN45	VN4058	687.65	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:38	1	adulto	activo	matorral de montaña	VN45	VN4058	687.38	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:33	1	adulto	escape	matorral de montaña	VN45	VN4058	682.59	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:28	1	adulto	activo	prado o pasto	VN45	VN4058	682.08	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:24	1	adulto	escape	prado o pasto	VN45	VN4058	679.27	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:22	1	adulto	activo	prado o pasto	VN45	VN4058	682.87	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:14	1	adulto	activo	matorral de montaña	VN45	VN4058	682.22	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:47	1	adulto	escape	matorral de montaña	VN45	VN4058	696.29	Quintanabaldo
Lacerta bilineata	8/4/2019	mediodía	13:42	1	adulto	activo	matorral de montaña	VN45	VN4058	697.27	Quintanabaldo
Lacerta bilineata	24/6/2019	mañana	08:11	1	joven	muerto	prado o pasto	VM68	VM6185	970.02	Arlanzón.
Lacerta bilineata	3/7/2019	tarde	19:21	1	adulto	escape	hayedo, robledal o frondosas	VN56	VN5668	733.30	Espinosa de los Monteros
Lacerta bilineata	3/7/2019	tarde	19:42	1	adulto	activo	prado o pasto	VN56	VN5768	720.96	Espinosa de los Monteros
Lacerta bilineata	3/7/2019	tarde	19:42	1	adulto	escape	prado o pasto	VN56	VN5768	720.64	Espinosa de los Monteros
Lacerta bilineata	3/7/2019	tarde	19:42	1	adulto	activo	prado o pasto	VN56	VN5768	721.42	Espinosa de los Monteros
Lacerta bilineata	3/7/2019	tarde	19:42	1	adulto	activo	prado o pasto	VN56	VN5768	721.56	Espinosa de los Monteros
Lacerta bilineata	3/7/2019	tarde	19:42	1	adulto	activo	prado o pasto	VN56	VN5768	721.34	Espinosa de los Monteros

Lacerta schreiberi Bedriaga, 1878

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Lacerta schreiberi	27/6/2017	mañana	11:36	1	adulto	escape	bosque de ribera	VN33	VN3433	685.11	San Felices del Rudrón
Lacerta schreiberi	27/6/2017	mañana	11	1	adulto	escape	matorral de montaña	VN33	VN3431	691.60	Covanera
Lacerta schreiberi	27/6/2017	mañana	10:48	1	adulto	escape	bosque de ribera	VN33	VN3431	697.93	Covanera
Lacerta schreiberi	27/6/2017	mañana	10:43	1	adulto	activo	matorral de montaña	VN33	VN3431	698.19	Covanera
Lacerta schreiberi	5/7/2019	tarde	16:05	1	adulto	escape	bosque de ribera	VN33	VN3431	695.32	Covanera

Género *Podarcis* Wagler, 1830

Podarcis liolepis (Boulenger, 1905)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Podarcis liolepis	3/7/2016	mañana	10:33	1	adulto	activo	muro de piedra	VM58	VM5586	929.26	Ibeas de Juarros
Podarcis liolepis	9/7/2016	mediodía	14:33	1	adulto	escape	cantera	VN40	VN4503	920.37	Villaverde de Peñahorada
Podarcis liolepis	9/7/2016	mediodía	12:38	1	adulto	escape	prado o pasto	VN51	VN5919	655.39	Lences

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Podarcis liolepis	16/7/2016	tarde	16:30	4	adulto	escape	muro de piedra	VM58	VM5586	928.29	Ibeas de Juarros
Podarcis liolepis	20/7/2016	tarde	19:39	1	muda		prado o pasto	VN40	VN4404	992.30	Ubierna
Podarcis liolepis	20/7/2016	tarde	16:43	1	adulto	escape	núcleo urbano	VM58	VM5586	930.41	Ibeas de Juarros
Podarcis liolepis	17/6/2017	mañana	11:29	1	adulto	activo	matorral de montaña	VN87	VN8379	324.14	Valle de Mena.
Podarcis liolepis	18/6/2017	tarde	15:41	1	adulto	activo	muro de piedra	VN46	VN4666	719.23	Quisicedo
Podarcis liolepis	18/6/2017	mediodía	13:41	1	adulto	activo	erial o roca a flor de tierra	VN46	VN4564	768.81	Merindad de Sotocueva
Podarcis liolepis	18/6/2017	mediodía	13:12	1	adulto	activo	encinar, alcornocal o dehesa	VN46	VN4664	751.08	Merindad de Sotocueva
Podarcis liolepis	18/6/2017	mañana	11:44	1	adulto	escape	erial o roca a flor de tierra	VN46	VN4664	782.59	Merindad de Sotocueva
Podarcis liolepis	19/6/2017	tarde	19:50	1	adulto	activo	matorral de montaña	VN57	VN5173	824.98	Las Machorras
Podarcis liolepis	19/6/2017	mañana	11:52	1	adulto	activo	muro de piedra	VN77	VN7275	359.69	Burceña
Podarcis liolepis	19/6/2017	mañana	11:13	1	adulto	activo	prado o pasto	VN76	VN7169	376.28	Lezana de Mena
Podarcis liolepis	19/6/2017	mañana	11:10	1	adulto	activo	prado o pasto	VN76	VN7169	376.36	Lezana de Mena
Podarcis liolepis	19/6/2017	mañana	11:03	1	adulto	termorregulación	muro de piedra	VN76	VN7169	374.79	Lezana de Mena
Podarcis liolepis	19/6/2017	mañana	09:57	1	adulto	activo	matorral de montaña	VN56	VN5869	747.49	Montecillo de Montija
Podarcis liolepis	19/6/2017	mañana	09:56	1	adulto	activo	matorral de montaña	VN56	VN5869	746.57	Montecillo de Montija
Podarcis liolepis	21/6/2017	mañana	11:20	1	adulto	activo	núcleo urbano	VN56	VN5569	753.87	Espinosa de los Monteros
Podarcis liolepis	23/6/2017	mediodía	12:49	1	adulto	escape	erial o roca a flor de tierra	VN43	VN4233	1098.48	Huidobro
Podarcis liolepis	24/6/2017	tarde	17:22	1	adulto	activo	matorral de montaña	VN35	VN3657	839.73	Soncillo
Podarcis liolepis	25/6/2017	mañana	11:31	1	adulto	escape	prado o pasto	VN40	VN4406	987.70	Gredilla la Polera
Podarcis liolepis	25/6/2017	mañana	11:26	1	adulto	activo	prado o pasto	VN40	VN4406	990.35	Gredilla la Polera
Podarcis liolepis	25/6/2017	mañana	11:37	1	adulto	activo	erial o roca a flor de tierra	VN40	VN4406	998.83	Gredilla la Polera
Podarcis liolepis	25/6/2017	mañana	10:38	1	adulto	activo	canchal, risco o acantilado	VN40	VN4405	985.63	Gredilla la Polera
Podarcis liolepis	25/6/2017	mañana	10:36	1	adulto	activo	canchal, risco o acantilado	VN40	VN4405	984.63	Gredilla la Polera
Podarcis liolepis	6/4/2019	mañana	10:49	1	adulto	termorregulación	muro de piedra	VN12	VN1828	910.92	Basconcillos del Tozo
Podarcis liolepis	19/6/2019	mañana	10:35	1	adulto	activo	encinar, alcornocal o dehesa	VM58	VM5887	1038.60	Ibeas de Juarros
Podarcis liolepis	4/7/2019	tarde	20:55	1	adulto	activo	turbera	VN25	VN2557	846.50	Arnedo

Podarcis muralis (Laurenti, 1768)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Podarcis muralis	16/6/2017	tarde	19:33	1	adulto	inactivo	prado o pasto	VN47	VN4674	982.96	Espinosa de los Monteros
Podarcis muralis	16/6/2017	tarde	18:39	1	adulto	escape	muro de piedra	VN47	VN4372	1095.64	Espinosa de los Monteros
Podarcis muralis	16/6/2017	tarde	19:02	1	adulto	activo	muro de piedra	VN47	VN4272	1169.32	Espinosa de los Monteros
Podarcis muralis	16/6/2017	mañana	10:26	1	adulto	activo	muro de piedra	VN47	VN4573	1013.40	Espinosa de los Monteros
Podarcis muralis	17/6/2017	mediodía	12:52	7	adulto	activo	muro de piedra	VN87	VN8576	218.52	San Pelayo, Ayega
Podarcis muralis	17/6/2017	mañana	08:53	1	adulto	inactivo	prado o pasto	VN87	VN8179	192.22	Santecilla
Podarcis muralis	18/6/2017	atardecer	20:41	1	adulto	activo	canchal, risco o acantilado	VN36	VN3663	703.63	Cidad de Valdeporres
Podarcis muralis	18/6/2017	tarde	18:21	1	adulto	activo	muro de piedra	VN36	VN3664	709.32	Busnela
Podarcis muralis	18/6/2017	tarde	18:27	1	adulto	activo	matorral de montaña	VN36	VN3664	710.26	Busnela
Podarcis muralis	18/6/2017	tarde	17:20	1	adulto	activo	matorral de montaña	VN36	VN3664	707.28	Busnela
Podarcis muralis	18/6/2017	tarde	17:20	1	adulto	activo	muro de piedra	VN36	VN3664	707.32	Busnela
Podarcis muralis	18/6/2017	tarde	17:18	1	adulto	escape	muro de piedra	VN36	VN3664	707.30	Busnela
Podarcis muralis	18/6/2017	tarde	17:18	1	adulto	alimentación	muro de piedra	VN36	VN3664	707.52	Busnela

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Podarcis muralis	18/6/2017	tarde	17:15	1	adulto	escape	muro de piedra	VN36	VN3664	707.00	Busnela
Podarcis muralis	18/6/2017	tarde	17:14	1	adulto	activo	muro de piedra	VN36	VN3664	707.13	Busnela
Podarcis muralis	18/6/2017	tarde	17:13	1	adulto	activo	matorral de montaña	VN36	VN3664	707.11	Busnela
Podarcis muralis	18/6/2017	tarde	17:12	1	adulto	termorregulación	matorral de montaña	VN36	VN3664	707.00	Busnela
Podarcis muralis	18/6/2017	tarde	17:12	1	adulto	activo	muro de piedra	VN36	VN3664	707.46	Busnela
Podarcis muralis	19/6/2017	tarde	18:06	1	adulto	activo	muro de piedra	VN47	VN4879	1164.48	Lunada
Podarcis muralis	19/6/2017	tarde	17:52	1	adulto	activo	matorral de montaña	VN48	VN4780	1277.16	Lunada
Podarcis muralis	19/6/2017	tarde	17:51	1	adulto	escape	muro de piedra	VN48	VN4780	1278.43	Lunada
Podarcis muralis	19/6/2017	tarde	17:50	1	adulto	activo	muro de piedra	VN48	VN4780	1278.70	Lunada
Podarcis muralis	19/6/2017	tarde	17:50	1	adulto	activo	muro de piedra	VN48	VN4780	1278.58	Lunada
Podarcis muralis	19/6/2017	tarde	17:49	1	adulto	activo	muro de piedra	VN48	VN4780	1279.02	Lunada
Podarcis muralis	19/6/2017	tarde	17:48	1	adulto	activo	muro de piedra	VN48	VN4780	1279.57	Lunada
Podarcis muralis	19/6/2017	tarde	17:47	1	adulto	activo	matorral de montaña	VN48	VN4780	1279.89	Lunada
Podarcis muralis	19/6/2017	tarde	17:47	1	adulto	escape	matorral de montaña	VN48	VN4780	1280.19	Lunada
Podarcis muralis	19/6/2017	tarde	17:46	1	adulto	escape	prado o pasto	VN48	VN4780	1280.43	Lunada
Podarcis muralis	19/6/2017	tarde	17:46	1	adulto	activo	prado o pasto	VN48	VN4780	1280.79	Lunada
Podarcis muralis	19/6/2017	tarde	17:46	1	adulto	escape	matorral de montaña	VN48	VN4780	1281.53	Lunada
Podarcis muralis	19/6/2017	tarde	17:45	1	adulto	activo	matorral de montaña	VN48	VN4780	1282.44	Lunada
Podarcis muralis	19/6/2017	tarde	17:45	1	adulto	escape	matorral de montaña	VN48	VN4780	1283.16	Lunada
Podarcis muralis	19/6/2017	tarde	17:43	1	adulto	escape	muro de piedra	VN48	VN4780	1336.70	Lunada
Podarcis muralis	19/6/2017	tarde	17:20	1	adulto	activo	muro de piedra	VN47	VN4679	1338.55	Lunada
Podarcis muralis	19/6/2017	tarde	17:13	1	adulto	escape	muro de piedra	VN47	VN4679	1334.90	Lunada
Podarcis muralis	19/6/2017	tarde	17:11	1	adulto	escape	muro de piedra	VN47	VN4679	1332.20	Lunada
Podarcis muralis	19/6/2017	tarde	17:11	1	adulto	activo	muro de piedra	VN47	VN4679	1331.83	Lunada
Podarcis muralis	19/6/2017	mediodía	12:11	1	adulto	termorregulación	muro de piedra	VN77	VN7576	354.64	Ribota de Ordunte
Podarcis muralis	19/6/2017	mañana	11:52	1	adulto	activo	muro de piedra	VN77	VN7275	359.76	Burceña
Podarcis muralis	19/6/2017	mañana	10:30	1	adulto	escape	muro de piedra	VN67	VN6373	800.94	Agüera
Podarcis muralis	19/6/2017	mañana	10:29	1	adulto	activo	muro de piedra	VN67	VN6373	800.96	Agüera
Podarcis muralis	19/6/2017	mañana	10:20	1	adulto	escape	matorral de montaña	VN67	VN6373	796.72	Agüera
Podarcis muralis	21/6/2017	tarde	20:21	1	adulto	activo	muro de piedra	VN95	VN9854	899.50	Monte Santiago
Podarcis muralis	21/6/2017	mediodía	13:31	1	adulto	activo	matorral de montaña	VN95	VN9954	841.15	Monte Santiago
Podarcis muralis	21/6/2017	mediodía	12:31	1	adulto	activo	muro de piedra	VN95	VN9954	842.24	Monte Santiago
Podarcis muralis	21/6/2017	mediodía	12:26	1	adulto	activo	muro de piedra	VN95	VN9954	841.54	Monte Santiago
Podarcis muralis	21/6/2017	mediodía	12:23	1	adulto	escape	prado o pasto	VN95	VN9954	841.95	Monte Santiago
Podarcis muralis	24/6/2017	tarde	14:42	1	adulto	activo	matorral de montaña	VN46	VN4667	871.06	Quisicedo
Podarcis muralis	24/6/2017	tarde	14:38	1	adulto	escape	matorral de montaña	VN46	VN4668	872.04	Quisicedo
Podarcis muralis	24/6/2017	tarde	14:38	1	adulto	escape	matorral de montaña	VN46	VN4668	872.04	Quisicedo
Podarcis muralis	24/6/2017	tarde	14:13	1	adulto	cortejo	matorral de montaña	VN46	VN4668	941.05	Quisicedo
Podarcis muralis	24/6/2017	tarde	14:13	1	adulto	cortejo	matorral de montaña	VN46	VN4668	941.05	Quisicedo
Podarcis muralis	24/6/2017	tarde	14:08	1	adulto	activo	muro de piedra	VN46	VN4668	945.04	Quisicedo
Podarcis muralis	24/6/2017	mediodía	13:18	1	adulto	activo	matorral de montaña	VN47	VN4770	1177.97	Quintanilla del Rebollar
Podarcis muralis	24/6/2017	mediodía	13:16	1	adulto	activo	matorral de montaña	VN47	VN4770	1168.79	Quintanilla del Rebollar
Podarcis muralis	24/6/2017	mediodía	13:11	1	adulto	activo	matorral de montaña	VN47	VN4770	1160.99	Quintanilla del Rebollar
Podarcis muralis	24/6/2017	mediodía	13:06	1	adulto	activo	matorral de montaña	VN47	VN4770	1170.09	Quintanilla del Rebollar
Podarcis muralis	24/6/2017	mediodía	12:43	1	adulto	activo	matorral de montaña	VN47	VN4772	1311.30	Espinosa de los Monteros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Podarcis muralis	26/6/2017	tarde	16:29	1	adulto	escape	matorral de montaña	VN56	VN5768	719.95	Espinosa de los Monteros
Podarcis muralis	26/6/2017	tarde	16:28	1	adulto	escape	matorral de montaña	VN56	VN5768	719.66	Espinosa de los Monteros
Podarcis muralis	26/6/2017	tarde	16:28	1	adulto	escape	matorral de montaña	VN56	VN5768	719.59	Espinosa de los Monteros
Podarcis muralis	26/6/2017	tarde	16:27	1	adulto	activo	matorral de montaña	VN56	VN5768	719.06	Espinosa de los Monteros
Podarcis muralis	26/6/2017	tarde	16:26	1	adulto	activo	matorral de montaña	VN56	VN5768	718.62	Espinosa de los Monteros
Podarcis muralis	26/7/2017	tarde	16:26	1	adulto	activo	matorral de montaña	VN56	VN5768	718.45	Espinosa de los Monteros
Podarcis muralis	4/7/2019	mediodía	13:47	1	adulto	activo	matorral de montaña	VN47	VN4373	1088.83	Espinosa de los Monteros

Género *Psammodromus* Fitzinger, 1826

Psammodromus algirus (Linnaeus, 1758)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Psammodromus algirus	30/6/2017	tarde	18:18	1	adulto	activo	matorral mediterráneo	VN51	VN5919	656.85	Lences

Género *Timon* Tschudi, 1836

Timon lepidus (Daudin, 1802)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Timon lepidus	9/7/2016	mediodía	14:13	1	adulto	Atropellado	matorral de montaña	VN40	VN4603	890.57	Peñahorada.
Timon lepidus	9/7/2016	mediodía	12:12	1	adulto	activo	cultivo de secano	VN52	VN5920	679.62	Lences
Timon lepidus	15/7/2016	mañana	11:15	1	adulto	escape	matorral de montaña	VM58	VM5887	1028.58	Ibeas de Juarros
Timon lepidus	16/7/2016	tarde	18:20	1	adulto	inactivo	cultivo de secano	VM68	VM6188	1001.09	Arlanzón.
Timon lepidus	18/6/2017	mediodía	12:19	1	joven	activo	encinar, alcornocal o dehesa	VM58	VM5788	991.70	Ibeas de Juarros
Timon lepidus	18/6/2017	mediodía	13:28	1	adulto	activo	muro de piedra	VN46	VN4564	762.48	Merindad de Sotocueva
Timon lepidus	18/6/2017	mediodía	12:42	1	adulto	activo	encinar, alcornocal o dehesa	VN46	VN4664	767.02	Merindad de Sotocueva
Timon lepidus	20/6/2017	tarde	19:58	1	muda		prado o pasto	VN40	VN4304	986.00	Ubierna
Timon lepidus	20/6/2017	tarde	19:28	1	adulto	inactivo	prado o pasto	VN40	VN4304	989.17	Ubierna
Timon lepidus	20/6/2017	tarde	15:56	1	adulto	inactivo	prado o pasto	VM58	VM5987	1011.82	Zalduendo
Timon lepidus	20/6/2017	tarde	15:47	1	adulto	inactivo	prado o pasto	VM58	VM5987	1011.61	Zalduendo
Timon lepidus	20/6/2017	mediodía	13:37	1	adulto	activo	matorral mediterráneo	VM58	VM5788	1002.88	Ibeas de Juarros
Timon lepidus	22/6/2017	tarde	20:36	1	adulto	muerto	prado o pasto	VN40	VN4306	1008.85	Gredilla la Polera
Timon lepidus	23/6/2017	mañana	11:19	1	adulto	activo	erial o roca a flor de tierra	VN43	VN4233	1095.62	Huidobro
Timon lepidus	25/6/2017	tarde	20:29	1	muda		prado o pasto	VN40	VN4305	1007.62	Ubierna
Timon lepidus	25/6/2017	tarde	17:34	1	adulto	activo	matorral mediterráneo	VM58	VM5888	1017.09	Zalduendo
Timon lepidus	25/6/2017	mañana	11:53	1	adulto	escape	prado o pasto	VN40	VN4306	1007.99	Gredilla la Polera
Timon lepidus	25/6/2017	mañana	10:09	1	adulto	activo	prado o pasto	VN40	VN4405	960.48	Gredilla la Polera
Timon lepidus	25/6/2017	mañana	09:23	1	joven	escape	encinar, alcornocal o dehesa	VN40	VN4306	1002.79	Gredilla la Polera
Timon lepidus	28/6/2017	tarde	17:42	1	joven	inactivo	matorral de montaña	VN33	VN3433	704.00	San Felices del Rudrón
Timon lepidus	30/6/2017	tarde	17:51	1	joven	activo	matorral mediterráneo	VN51	VN5919	656.84	Lences
Timon lepidus	2/7/2017	mañana	11:12	1	adulto	activo	matorral mediterráneo	VM58	VM5788	1000.41	Ibeas de Juarros
Timon lepidus	18/6/2019	mañana	10:37	1	adulto	escape	encinar, alcornocal o dehesa	VM58	VM5887	1037.77	Ibeas de Juarros
Timon lepidus	5/7/2019	tarde	18:44	1	joven	inactivo	prado o pasto	VN43	VN4234	1082.64	Huidobro

Género *Zootoca* Wagler, 1830

Zootoca vivipara (Jacquin, 1787)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Zootoca vivipara	16/6/2017	tarde	16:19	1	joven	activo	prado o pasto	VN47	VN4373	1118.29	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	16:19	1	joven	activo	prado o pasto	VN47	VN4373	1118.28	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:20	1	adulto	activo	turbera	VN47	VN4373	1096.02	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:20	1	adulto	escape	turbera	VN47	VN4373	1096.02	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:20	1	adulto	escape	turbera	VN47	VN4373	1096.00	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:11	1	adulto	escape	turbera	VN47	VN4373	1100.10	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:11	1	joven	activo	turbera	VN47	VN4373	1100.24	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:11	1	adulto	escape	turbera	VN47	VN4373	1100.45	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:11	1	joven	escape	turbera	VN47	VN4373	1100.07	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:07	1	adulto	activo	turbera	VN47	VN4373	1107.98	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:07	1	adulto	activo	turbera	VN47	VN4373	1107.65	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:52	1	adulto	activo	turbera	VN47	VN4274	1154.02	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:49	1	adulto	activo	turbera	VN47	VN4274	1156.70	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:49	1	adulto	escape	turbera	VN47	VN4274	1156.63	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:49	1	adulto	escape	turbera	VN47	VN4274	1156.66	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:44	1	adulto	activo	turbera	VN47	VN4274	1158.22	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:41	1	adulto	escape	turbera	VN47	VN4274	1158.50	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:31	1	adulto	escape	turbera	VN47	VN4274	1157.88	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:31	1	adulto	termorregulación	turbera	VN47	VN4274	1157.76	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:30	1	adulto	activo	turbera	VN47	VN4274	1157.98	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:29	1	adulto	escape	turbera	VN47	VN4274	1158.19	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:29	1	adulto	activo	turbera	VN47	VN4274	1158.21	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:29	1	adulto	activo	turbera	VN47	VN4274	1158.13	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:27	1	adulto	escape	prado o pasto	VN47	VN4274	1158.40	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:27	1	adulto	activo	prado o pasto	VN47	VN4274	1158.23	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:26	1	adulto	escape	prado o pasto	VN47	VN4274	1157.70	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:25	1	adulto	escape	prado o pasto	VN47	VN4274	1157.34	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:23	1	adulto	escape	prado o pasto	VN47	VN4274	1156.43	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	mediodía	12:23	1	adulto	activo	prado o pasto	VN47	VN4274	1156.40	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	16:17	1	adulto	escape	prado o pasto	VN47	VN4373	1118.82	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	16:16	1	adulto	escape	prado o pasto	VN47	VN4373	1119.48	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	15:56	1	adulto	activo	turbera	VN47	VN4373	1120.91	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:14	1	adulto	termorregulación	turbera	VN47	VN4373	1095.11	Espinosa de los Monteros
Zootoca vivipara	16/6/2017	tarde	14:12	1	adulto	activo	turbera	VN47	VN4373	1098.01	Espinosa de los Monteros
Zootoca vivipara	19/6/2017	tarde	17:28	1	adulto	activo	prado o pasto	VN47	VN4679	1331.16	Lunada
Zootoca vivipara	19/6/2017	tarde	17:20	1	adulto	activo	muro de piedra	VN47	VN4679	1336.42	Lunada
Zootoca vivipara	19/6/2017	tarde	17:09	1	adulto	activo	matorral de montaña	VN48	VN4780	1279.75	Lunada
Zootoca vivipara	19/6/2017	tarde	16:56	1	adulto	escape	matorral de montaña	VN47	VN4679	1325.26	Lunada
Zootoca vivipara	29/6/2017	tarde	19:15	1	huevo		matorral de montaña	VN47	VN4373	1119.02	Espinosa de los Monteros
Zootoca vivipara	29/6/2017	tarde	19:02	1	huevo		prado o pasto	VN47	VN4273	1139.32	Espinosa de los Monteros
Zootoca vivipara	29/6/2017	tarde	18:49	1	adulto	inactivo	prado o pasto	VN47	VN4274	1156.90	Espinosa de los Monteros
Zootoca vivipara	29/6/2017	tarde	18:42	1	adulto	inactivo	prado o pasto	VN47	VN4274	1147.76	Espinosa de los Monteros

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Zootoca vivipara	4/7/2019	mañana	10:43	1	adulto	inactivo	turbera	VN47	VN4373	1113.76	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:39	1	adulto	inactivo	turbera	VN47	VN4373	1118.51	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:37	1	adulto	escape	turbera	VN47	VN4373	1122.06	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:37	1	adulto	inactivo	turbera	VN47	VN4373	1122.35	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:34	1	adulto	escape	turbera	VN47	VN4373	1123.16	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:33	1	adulto	escape	turbera	VN47	VN4373	1123.55	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:33	1	adulto	escape	turbera	VN47	VN4373	1124.18	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:26	1	adulto	escape	turbera	VN47	VN4373	1125.99	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:23	1	adulto	escape	turbera	VN47	VN4373	1126.32	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:18	1	adulto	escape	turbera	VN47	VN4373	1124.93	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	09:56	1	huevo		turbera	VN47	VN4373	1120.86	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	09:55	1	huevo		turbera	VN47	VN4373	1120.87	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	09:55	1	huevo		turbera	VN47	VN4373	1120.97	Espinosa de los Monteros
Zootoca vivipara	4/7/2019	mañana	10:05	1	adulto	inactivo	turbera	VN47	VN4373	1119.58	Espinosa de los Monteros

Familia Colubridae Oppel, 1811

Género *Coronella* Laurenti, 1768

Coronella austriaca Laurenti, 1768

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Coronella austriaca	9/7/2016	mañana	11:15	1	joven	muerto	prado o pasto	VN42	VN4822	1056.15	Cernégula
Coronella austriaca	18/6/2017	atardecer	20:35	1	muda		matorral de montaña	VN36	VN3663	701.76	Cidad de Valdeporres
Coronella austriaca	18/6/2017	tarde	17:37	1	joven	activo	matorral de montaña	VN36	VN3664	707.21	Busnela
Coronella austriaca	3/7/2019	tarde	19:49	1	joven	inactivo	prado o pasto	VN56	VN5768	716.41	Espinosa de los Monteros
Coronella austriaca	3/7/2019	atardecer	21:48	1	adulto	inactivo	prado o pasto	VN56	VN5768	705.00	Espinosa de los Monteros
Coronella austriaca	5/7/2019	mañana	09:56	1	adulto	termorregulación	matorral de montaña	VN25	VN2558	898.32	Herbosa

Coronella girondica (Daudin, 1803)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Coronella girondica	9/7/2016	mañana	10:03	1	adulto	Atropellado	cultivo de secano	VN42	VN4820	975.44	Cernégula
Coronella girondica	18/6/2017	mediodía	13:21	1	muda		encinar, alcornocal o dehesa	VN46	VN4664	753.28	Merindad de Sotocueva
Coronella girondica	18/6/2017	mediodía	12:01	1	adulto	activo	encinar, alcornocal o dehesa	VN46	VN4664	769.29	Merindad de Sotocueva
Coronella girondica	20/6/2017	noche	00:27	1	adulto	activo	matorral de montaña	VN56	VN5164	651.14	Hornillalastra
Coronella girondica	21/6/2017	noche	01:01	1	adulto	Atropellado	matorral de montaña	VN55	VN5658	687.12	Barruso
Coronella girondica	30/6/2017	tarde	19:58	1	huevo		balsa	VN42	VN4723	1019.87	Cernégula
Coronella girondica	2/7/2017	mañana	11:03	1	adulto	escape	matorral mediterráneo	VM58	VM5788	1001.85	Ibeas de Juarros
Coronella girondica	18/7/2017	mañana	11:09	1	adulto	escape	cantera	VM58	VM5788	1001.45	Ibeas de Juarros

Género *Natrix* Laurenti, 1768

Natrix maura (Linnaeus, 1758)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Natrix maura	14/7/2016	mediodía	11:18	3	joven	activo	charca	VM58	VM5987	1010.81	Zalduendo
Natrix maura	16/6/2017	tarde	16:12	1	adulto	escape	arroyo	VN47	VN4373	1119.81	Espinosa de los Monteros
Natrix maura	18/6/2017	noche	23:36	1	adulto	activo	balsa	VN56	VN5668	732.13	Espinosa de los Monteros,
Natrix maura	19/6/2017	noche	23:55	1	joven	activo	balsa	VN56	VN5569	746.58	Espinosa de los Monteros
Natrix maura	20/6/2017	noche	23:50	1	joven	activo	lago o pantano	VN42	VN4820	981.99	Cernégula
Natrix maura	20/6/2017	noche	23:07	1	joven	activo	balsa	VN42	VN4821	982.39	Cernégula
Natrix maura	20/6/2017	noche	22:53	1	joven	activo	lago o pantano	VN42	VN4820	981.76	Cernégula
Natrix maura	20/6/2017	atardecer	21:53	1	joven	activo	prado o pasto	VN42	VN4622	1013.44	Cernégula
Natrix maura	25/6/2017	mediodía	13:48	1	adulto	activo	lago o pantano	VN42	VN4820	982.28	Cernégula
Natrix maura	25/6/2017	mediodía	12:43	1	joven	activo	balsa	VN42	VN4821	990.35	Cernégula
Natrix maura	25/6/2017	mediodía	12:48	1	joven	escape	balsa	VN42	VN4820	982.02	Cernégula
Natrix maura	25/6/2017	mediodía	12:47	1	joven	escape	balsa	VN42	VN4820	982.22	Cernégula
Natrix maura	25/6/2017	mediodía	12:46	1	joven	activo	balsa	VN42	VN4820	982.09	Cernégula
Natrix maura	27/6/2017	mañana	10:54	1	adulto	termorregulación	bosque de ribera	VN33	VN3431	696.98	Covanera
Natrix maura	27/6/2017	mañana	10:16	1	adulto	activo	rio o canal	VN33	VN3431	693.33	Covanera
Natrix maura	28/6/2017	atardecer	21:11	1	joven	activo	balsa	VN22	VN2326	983.76	Trashaedo del Tozo
Natrix maura	28/6/2017	atardecer	21:18	1	joven	activo	balsa	VN22	VN2326	983.08	Trashaedo del Tozo
Natrix maura	4/7/2017	mañana	11:47	1	adulto	activo	bosque de ribera	VM58	VM5686	931.21	Ibeas de Juarros
Natrix maura	4/7/2017	mañana	11:26	1	joven	activo	bosque de ribera	VM58	VM5686	931.25	Ibeas de Juarros
Natrix maura	17/6/2019	tarde	19:03	1	adulto	activo	balsa	VM68	VM6185	971.36	Arlanzón.
Natrix maura	18/6/2019	mañana	09:32	1	adulto	activo	encinar, alcornocal o dehesa	VM58	VM5788	1005.60	Ibeas de Juarros

Natrix astreptophora (López-Seoane, 1884)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Natrix astreptophora	14/7/2016	mediodía	11:01	1	joven	activo	charca	VM58	VM5987	1010.81	Zalduendo
Natrix astreptophora	17/6/2017	mediodía	12:06	1	adulto	escape	prado o pasto	VN87	VN8577	239.64	Orrantia, Ayega
Natrix astreptophora	18/6/2017	tarde	19:31	1	joven	inactivo	prado o pasto	VN36	VN3664	806.21	Busnela
Natrix astreptophora	18/6/2017	tarde	17:31	1	joven	escape	matorral de montaña	VN36	VN3664	707.33	Busnela
Natrix astreptophora	18/6/2017	tarde	15:49	1	joven	activo	rio o canal	VN46	VN4666	720.43	Quisicedo
Natrix astreptophora	18/6/2017	tarde	15:33	1	adulto	activo	bosque de ribera	VN46	VN4565	712.05	Merindad de Sotocueva
Natrix astreptophora	21/6/2017	tarde	14:39	1	joven	activo	rio o canal	VN95	VN9954	836.99	Monte Santiago
Natrix astreptophora	25/6/2017	mediodía	13:58	1	joven	inactivo	balsa	VN42	VN4821	982.58	Cernégula
Natrix astreptophora	28/6/2017	tarde	20:29	1	adulto	activo	lago o pantano	VN12	VN1827	914.81	Basconcillos del Tozo
Natrix astreptophora	28/6/2017	tarde	18:36	1	joven	muerto	balsa	VN23	VN2833	1009.00	Ayoluengo
Natrix astreptophora	3/7/2017	mañana	11:35	1	adulto	activo	rio o canal	VM58	VM5686	931.82	Ibeas de Juarros
Natrix astreptophora	8/4/2019	mañana	11:48	1	joven	activo	balsa	VN25	VN2857	909.80	Villamediana de San Román
Natrix astreptophora	3/7/2019	atardecer	20:55	1	joven	inactivo	prado o pasto	VN56	VN5768	711.10	Espinosa de los Monteros

Familia Viperidae Oppel, 1811

Género *Vipera* Laurenti, 1768

Vipera aspis (Linnaeus, 1758)

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Vipera aspis	18/6/2017	mediodía	13:01	1	adulto	escape	encinar, alcornocal o dehesa	VN46	VN4664	753.63	Merindad de Sotocueva
Vipera aspis	23/6/2017	mañana	11:31	1	adulto	termorregulación	erial o roca a flor de tierra	VN43	VN4333	1096.11	Huidobro
Vipera aspis	6/4/2019	tarde	14:38	1	adulto	activo	encinar, alcornocal o dehesa	VN33	VN3433	766.39	San Felices del Rudrón

Vipera latastei Boscá, 1878

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Vipera latastei	2/7/2016	tarde	19:24	2	adulto	inactivo	matorral de montaña	VM58	VM5788	1002.41	Ibeas de Juarros
Vipera latastei	20/7/2016	tarde	20:11	1	adulto	inactivo	prado o pasto	VN40	VN4304	986.89	Ubierna
Vipera latastei	21/7/2016	tarde	20:10	1	adulto	inactivo	prado o pasto	VN40	VN4406	1000.45	Gredilla la Polera
Vipera latastei	21/7/2016	tarde	18:55	1	muda		prado o pasto	VN40	VN4406	1005.75	Gredilla la Polera
Vipera latastei	20/6/2017	mañana	09:18	1	joven	termorregulación	cantera	VM58	VM5788	1000.07	Ibeas de Juarros
Vipera latastei	22/6/2017	atardecer	21:11	1	adulto	inactivo	encinar, alcornocal o dehesa	VN40	VN4405	993.38	Gredilla la Polera
Vipera latastei	25/6/2017	tarde	20:55	1	muda		prado o pasto	VN40	VN4305	1024.54	Ubierna
Vipera latastei	18/7/2017	mediodía	12:33	1	adulto	activo	encinar, alcornocal o dehesa	VM58	VM5788	1000.16	Ibeas de Juarros
Vipera latastei	18/6/2019	mañana	10:43	1	joven	termorregulación	muro de piedra	VM58	VM5887	1031.33	Ibeas de Juarros
Vipera latastei	19/6/2019	mañana	09:09	1	joven	inactivo	cantera	VM58	VM5788	1006.83	Ibeas de Juarros
Vipera latastei	19/6/2019	mediodía	13:38	1	adulto	termorregulación	muro de piedra	VM58	VM5887	1031.49	Ibeas de Juarros
Vipera latastei	21/6/2019	mediodía	12:18	1	adulto	gregarismo	encinar, alcornocal o dehesa	VM58	VM5887	991.28	Ibeas de Juarros
Vipera latastei	5/7/2019	tarde	16:19	1	adulto	activo	bosque de ribera	VN33	VN3431	704.46	Covanera

Vipera seoanei Lataste, 1879

Especie	Fecha	Periodo	Hora	Ejemplares	Estadio	Conducta	Habitat	UTM 10Km.	UTM 1Km.	Altitud	Localidad
Vipera seoanei	16/6/2017	mediodía	13:06	1	adulto	escape	turbera	VN47	VN4274	1150.78	Espinosa de los Monteros
Vipera seoanei	17/6/2017	mediodía	12:38	1	adulto	escape	matorral de montaña	VN87	VN8677	182.05	Arza, Ayega
Vipera seoanei	18/6/2017	atardecer	20:05	1	adulto	escape	matorral de montaña	VN36	VN3663	701.26	Cidad de Valdeporres
Vipera seoanei	22/6/2017	mañana	08:32	1	adulto	inactivo	prado o pasto	VN12	VN1828	905.21	Basconcillos del Tozo
Vipera seoanei	26/6/2017	mediodía	12:40	1	adulto	activo	prado o pasto	VN56	VN5768	720.71	Espinosa de los Monteros
Vipera seoanei	27/6/2017	tarde	15:44	1	adulto	Atropellado	matorral de montaña	VN43	VN4033	1005.78	Nocedo
Vipera seoanei	6/4/2019	tarde	18:20	1	adulto	activo	matorral de montaña	VN25	VN2558	895.04	Herbosa
Vipera seoanei	8/4/2019	mediodía	13:21	1	adulto	activo	matorral de montaña	VN45	VN4058	699.36	Quintanabaldo
Vipera seoanei	4/7/2019	mañana	11:01	1	adulto	muerto	turbera	VN47	VN4373	1118.37	Espinosa de los Monteros
Vipera seoanei	5/7/2019	mañana	10:31	1	adulto	termorregulación	matorral de montaña	VN25	VN2558	889.85	Herbosa

Appendix 6.B - Fotografías de herpetofauna de la provincia de Burgos

Salamandra salamandra

Triturus marmoratus

Ichthyosaura alpestris

Lissotriton helveticus

Alytes obstetricans

Pelobates cultripes

Pelodytes punctatus

Hyla molleri

Bufo spinosus

Epidalea calamita

Rana temporaria

Pelophylax perezi

Mauremys leprosa

Anguis fragilis

Chalcides striatus

Lacerta bilineata

Podarcis liolepis

Podarcis muralis

Psammodromus algirus

Timon lepidus

Zootoca vivipara

Coronella austriaca

Coronella girondica

Natrix astreptophora

Natrix maura

Vipera aspis

Vipera latastei

Vipera latastei

Vipera latastei

Vipera latastei

Vipera seoanei

Vipera seoanei

Vipera seoanei

Appendix 7 - Genetic data set for *Chalcides ocellatus*

Species	**Sample code**	**Country**	***cytb***	**Reference**
C. ocellatus	CN12564	Spain	MN509445	This thesis
C. ocellatus	CN12645	Spain	MN509446	This thesis
C. ocellatus	CN13391	Spain	MN509447	This thesis
C. ocellatus	CN13434	Spain	MN509448	This thesis
C. ocellatus	CN13435	Spain	MN509449	This thesis
C. ocellatus	BEV.11048	Algeria	KY274233	Beddek et al., 2018
C. ocellatus	BEV.13254	Algeria	KY274205	Beddek et al., 2018
C. ocellatus	BEV.13611	Algeria	KY274209	Beddek et al., 2018
C. ocellatus	BEV.9200	Algeria	KY274241	Beddek et al., 2018
C. ocellatus	BEV.9203	Algeria	KY274243	Beddek et al., 2018
C. ocellatus	BEV.9227	Algeria	KY274242	Beddek et al., 2018
C. ocellatus	BEV.9255	Algeria	KY274247	Beddek et al., 2018
C. ocellatus	BEV.T1608	Algeria	KY274234	Beddek et al., 2018
C. ocellatus	BEV.T1609	Algeria	KY274235	Beddek et al., 2018
C. ocellatus	BEV.T4125	Algeria	KY274236	Beddek et al., 2018
C. ocellatus	BEV.T4216	Algeria	KY274250	Beddek et al., 2018
C. ocellatus	BEV.T4220	Algeria	KY274237	Beddek et al., 2018
C. ocellatus	BEV.T4225	Algeria	KY274238	Beddek et al., 2018
C. ocellatus	BEV.T4231	Algeria	KY274239	Beddek et al., 2018
C. ocellatus	BEV.T4242	Algeria	KY274240	Beddek et al., 2018
C. ocellatus	BEV.T633	Algeria	KY274244	Beddek et al., 2018
C. ocellatus	BEV.T635	Algeria	KY274245	Beddek et al., 2018
C. ocellatus	BEV.T637	Algeria	KY274246	Beddek et al., 2018
C. ocellatus	BEV.T6500	Algeria	KY274248	Beddek et al., 2018
C. ocellatus	BEV.T6839	Algeria	KY274249	Beddek et al., 2018
C. ocellatus	BEV.T7918	Algeria	KY274229	Beddek et al., 2018
C. ocellatus	BEV.T8026	Algeria	KY274228	Beddek et al., 2018
C. ocellatus	BEV.T8027	Algeria	KY274227	Beddek et al., 2018
C. ocellatus	BEV.T8028	Algeria	KY274226	Beddek et al., 2018
C. ocellatus	BEV.T8029	Algeria	KY274225	Beddek et al., 2018
C. ocellatus	BEV.T8030	Algeria	KY274224	Beddek et al., 2018
C. ocellatus	BEV.T8031	Algeria	KY274223	Beddek et al., 2018

Species	**Sample code**	**Country**	***cytb***	**Reference**
C. ocellatus	BEV.T8032	Algeria	KY274222	Beddek et al., 2018
C. ocellatus	BEV.T8033	Algeria	KY274221	Beddek et al., 2018
C. ocellatus	BEV.T8034	Algeria	KY274220	Beddek et al., 2018
C. ocellatus	BEV.T8035	Algeria	KY274219	Beddek et al., 2018
C. ocellatus	BEV.T8037	Algeria	KY274211	Beddek et al., 2018
C. ocellatus	BEV.T8038	Algeria	KY274218	Beddek et al., 2018
C. ocellatus	BEV.T8039	Algeria	KY274217	Beddek et al., 2018
C. ocellatus	BEV.T8041	Algeria	KY274216	Beddek et al., 2018
C. ocellatus	BEV.T8042	Algeria	KY274215	Beddek et al., 2018
C. ocellatus	BEV.T8043	Algeria	KY274214	Beddek et al., 2018
C. ocellatus	BEV.T8044	Algeria	KY274213	Beddek et al., 2018
C. ocellatus	BEV.T8045	Algeria	KY274212	Beddek et al., 2018
C. ocellatus	BEV.T8064	Algeria	KY274230	Beddek et al., 2018
C. ocellatus	BEV.T9407	Algeria	KY274231	Beddek et al., 2018
C. ocellatus	BEV.T9548	Algeria	KY274210	Beddek et al., 2018
C. ocellatus	BEV.T9580	Algeria	KY274208	Beddek et al., 2018
C. ocellatus	CN10018	Chafarinas Islands	KY614282	Martín et al., 2017
C. ocellatus	CN10019	Chafarinas Islands	KY614281	Martín et al., 2017
C. ocellatus	CN10020	Chafarinas Islands	KY614280	Martín et al., 2017
C. ocellatus	c010	Tunisia	FJ980213	Kornilios et al., 2010
C. ocellatus	c013	Tunisia	FJ980214	Kornilios et al., 2010
C. ocellatus	c014	Libya	FJ980215	Kornilios et al., 2010
C. ocellatus	c016	Tunisia	FJ980216	Kornilios et al., 2010
C. ocellatus	c025	Italy	FJ980217	Kornilios et al., 2010
C. ocellatus	c029	Libya	FJ980218	Kornilios et al., 2010
C. ocellatus	c030	Libya	FJ980219	Kornilios et al., 2010
C. ocellatus	c031	Libya	FJ980220	Kornilios et al., 2010
C. ocellatus	c033	Libya	FJ980221	Kornilios et al., 2010
C. ocellatus	c034	Libya	FJ980222	Kornilios et al., 2010
C. ocellatus	c035	Libya	FJ980223	Kornilios et al., 2010
C. ocellatus	c036	Libya	FJ980224	Kornilios et al., 2010
C. ocellatus	c037	Libya	FJ980225	Kornilios et al., 2010
C. ocellatus	c038	Libya	FJ980226	Kornilios et al., 2010

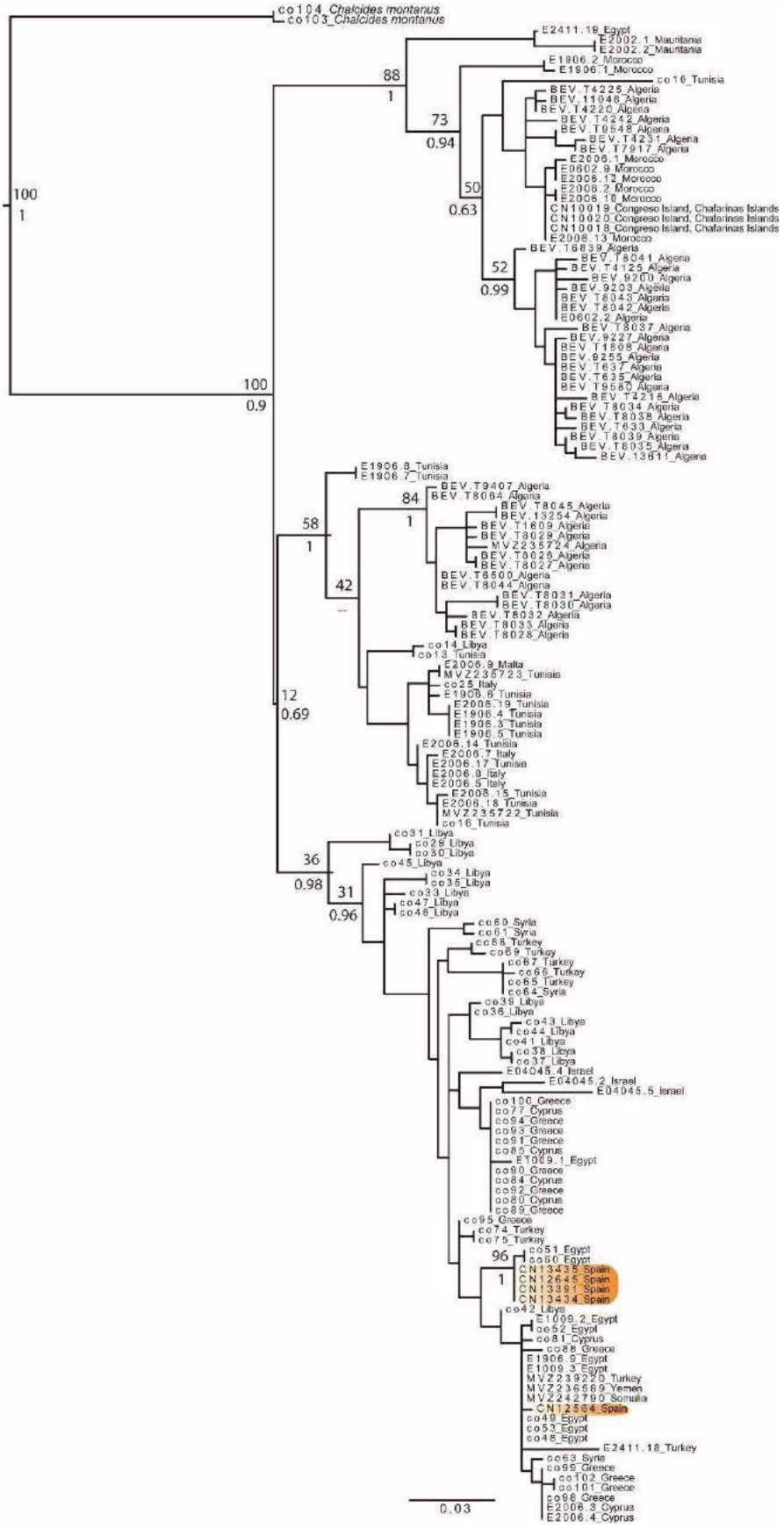
Species	**Sample code**	**Country**	***cytb***	**Reference**
C. ocellatus	c039	Libya	FJ980227	Kornilios et al., 2010
C. ocellatus	c041	Libya	FJ980228	Kornilios et al., 2010
C. ocellatus	c042	Libya	FJ980229	Kornilios et al., 2010
C. ocellatus	c043	Libya	FJ980230	Kornilios et al., 2010
C. ocellatus	c044	Libya	FJ980231	Kornilios et al., 2010
C. ocellatus	c045	Libya	FJ980232	Kornilios et al., 2010
C. ocellatus	c046	Libya	FJ980233	Kornilios et al., 2010
C. ocellatus	c047	Libya	FJ980234	Kornilios et al., 2010
C. ocellatus	c048	Egypt	FJ980235	Kornilios et al., 2010
C. ocellatus	c049	Egypt	FJ980236	Kornilios et al., 2010
C. ocellatus	c050	Egypt	FJ980237	Kornilios et al., 2010
C. ocellatus	c051	Egypt	FJ980238	Kornilios et al., 2010
C. ocellatus	c052	Egypt	FJ980239	Kornilios et al., 2010
C. ocellatus	c053	Egypt	FJ980240	Kornilios et al., 2010
C. ocellatus	c060	Syria	FJ980241	Kornilios et al., 2010
C. ocellatus	c061	Syria	FJ980242	Kornilios et al., 2010
C. ocellatus	c063	Syria	FJ980243	Kornilios et al., 2010
C. ocellatus	c064	Syria	FJ980244	Kornilios et al., 2010
C. ocellatus	c065	Turkey	FJ980245	Kornilios et al., 2010
C. ocellatus	c066	Turkey	FJ980246	Kornilios et al., 2010
C. ocellatus	c067	Turkey	FJ980247	Kornilios et al., 2010
C. ocellatus	c068	Turkey	FJ980248	Kornilios et al., 2010
C. ocellatus	c069	Turkey	FJ980249	Kornilios et al., 2010
C. ocellatus	c074	Turkey	FJ980250	Kornilios et al., 2010
C. ocellatus	c075	Turkey	FJ980251	Kornilios et al., 2010
C. ocellatus	c077	Cyprus	FJ980253	Kornilios et al., 2010
C. ocellatus	c080	Cyprus	FJ980254	Kornilios et al., 2010
C. ocellatus	c081	Cyprus	FJ980255	Kornilios et al., 2010
C. ocellatus	c084	Cyprus	FJ980256	Kornilios et al., 2010
C. ocellatus	c085	Cyprus	FJ980257	Kornilios et al., 2010
C. ocellatus	c088	Greece	FJ980258	Kornilios et al., 2010
C. ocellatus	c089	Greece	FJ980259	Kornilios et al., 2010
C. ocellatus	c090	Greece	FJ980260	Kornilios et al., 2010
C. ocellatus	c091	Greece	FJ980261	Kornilios et al., 2010

Species	**Sample code**	**Country**	***cytb***	**Reference**
C. ocellatus	c092	Greece	FJ980262	Kornilios et al., 2010
C. ocellatus	c093	Greece	FJ980263	Kornilios et al., 2010
C. ocellatus	c094	Greece	FJ980264	Kornilios et al., 2010
C. ocellatus	c095	Greece	FJ980265	Kornilios et al., 2010
C. ocellatus	c098	Greece	FJ980266	Kornilios et al., 2010
C. ocellatus	c099	Greece	FJ980267	Kornilios et al., 2010
C. ocellatus	c0100	Greece	FJ980268	Kornilios et al., 2010
C. ocellatus	c0101	Greece	FJ980269	Kornilios et al., 2010
C. ocellatus	c0102	Greece	FJ980270	Kornilios et al., 2010
C. ocellatus	E04045.2	Israel	EU278182	Carranza et al., 2008
C. ocellatus	E04045.4	Israel	EU278183	Carranza et al., 2008
C. ocellatus	E04045.5	Israel	EU278184	Carranza et al., 2008
C. ocellatus	E0602.2	Algeria	EU278169	Carranza et al., 2008
C. ocellatus	E0602.9	Morocco	EU278164	Carranza et al., 2008
C. ocellatus	E1009.1	Egypt	EU278181	Carranza et al., 2008
C. ocellatus	E1009.2	Egypt	EU278179	Carranza et al., 2008
C. ocellatus	E1009.3	Egypt	EU278177	Carranza et al., 2008
C. ocellatus	E1906.1	Morocco	EU278170	Carranza et al., 2008
C. ocellatus	E1906.2	Morocco	EU278171	Carranza et al., 2008
C. ocellatus	E1906.3	Tunisia	EU278194	Carranza et al., 2008
C. ocellatus	E1906.4	Tunisia	EU278195	Carranza et al., 2008
C. ocellatus	E1906.5	Tunisia	EU278196	Carranza et al., 2008
C. ocellatus	E1906.6	Tunisia	EU278193	Carranza et al., 2008
C. ocellatus	E1906.7	Tunisia	EU278198	Carranza et al., 2008
C. ocellatus	E1906.8	Tunisia	EU278199	Carranza et al., 2008
C. ocellatus	E1906.9	Egypt	EU278178	Carranza et al., 2008
C. ocellatus	E2002.1	Mauritania	EU278173	Carranza et al., 2008
C. ocellatus	E2002.2	Mauritania	EU278174	Carranza et al., 2008
C. ocellatus	E2006.1	Morocco	EU278165	Carranza et al., 2008
C. ocellatus	E2006.10	Morocco	EU278166	Carranza et al., 2008
C. ocellatus	E2006.12	Morocco	EU278163	Carranza et al., 2008
C. ocellatus	E2006.13	Morocco	EU278167	Carranza et al., 2008
C. ocellatus	E2006.14	Tunisia	EU278188	Carranza et al., 2008
C. ocellatus	E2006.15	Tunisia	EU278190	Carranza et al., 2008

Species	**Sample code**	**Country**	***cytb***	**Reference**
C. ocellatus	E2006.17	Tunisia	EU278189	Carranza et al., 2008
C. ocellatus	E2006.18	Tunisia	EU278191	Carranza et al., 2008
C. ocellatus	E2006.19	Tunisia	EU278197	Carranza et al., 2008
C. ocellatus	E2006.2	Morocco	EU278168	Carranza et al., 2008
C. ocellatus	E2006.3	Cyprus	EU278175	Carranza et al., 2008
C. ocellatus	E2006.4	Cyprus	EU278176	Carranza et al., 2008
C. ocellatus	E2006.5	Italy	EU278185	Carranza et al., 2008
C. ocellatus	E2006.7	Italy	EU278187	Carranza et al., 2008
C. ocellatus	E2006.8	Italy	EU278186	Carranza et al., 2008
C. ocellatus	E2006.9	Malta	EU278192	Carranza et al., 2008
C. ocellatus	E2411.18	Turkey	EU278180	Carranza et al., 2008
C. ocellatus	E2411.19	Egypt	EU278172	Carranza et al., 2008
C. ocellatus	MVZ:235722	Tunisia	JQ344285	Lavin and Papenfuss, 2012
C. ocellatus	MVZ:235723	Tunisia	JQ344284	Lavin and Papenfuss, 2012
C. ocellatus	MVZ:235724	Algeria	JQ344286	Lavin and Papenfuss, 2012
C. ocellatus	MVZ:236589	Yemen	JQ344283	Lavin and Papenfuss, 2012
C. ocellatus	MVZ:239220	Turkey	JQ344282	Lavin and Papenfuss, 2012
C. ocellatus	MVZ:242790	Somalia	JQ344290	Lavin and Papenfuss, 2012
C. montanus	c0103	Morocco	FJ980271	Kornilios et al., 2010
C. montanus	c0104	Morocco	FJ980272	Kornilios et al., 2010

Supplementary Table 6.S1.- Specimens used in the genetic analyses and related GenBank accession codes.

Appendix 8 - Cytochrome *b* Maximum likelihood phylogenetic tree



Supplementary Figure 6.S1.- Cytochrome *b* Maximum likelihood phylogenetic tree of *Chalcides ocellatus*. Bootstrap (ML) and Bayesian posterior probabilities (BI) support values are indicated above and below the nodes, respectively. The newly discovered Iberian specimens collected from Serra del Molar, Elx are highlighted. Sample codes and localities correlate to specimens in Appendix 7.

Appendix 9 - Published papers

En las siguientes páginas (302-353) se incluyen los artículos ya publicados y extraídos de los Capítulos 1, 3 y 6 de esta tesis doctoral, en la versión editorial de las revistas.

In the following pages (302-353) are included the scientific manuscripts already published and related to Chapters 1, 3 and 6 of this doctoral thesis, maintain with the journal editions.

En les següents pàgines (302-353) s'inclouen els articles ja publicats i extrets dels Capítols 1, 3 i 6 d'aquesta tesi doctoral, en la versió editorial de les revistes.

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Long-term changes in composition and distribution patterns in the Iberian herpetofaunal communities since the latest Pleistocene

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ABSTRACT

The climate has undergone significant changes since the end of the Last Glacial Maximum and in the course of the Holocene, parallel to important cultural transformations and migrations in the human communities. The faunal record has also suffered the effects of climate change. Amphibians and reptiles in particular have been shown to be highly sensitive because they are very susceptible to temperature alterations due to their ectothermy. This research presents the first approach to the Iberian paleobiogeography of the different species of amphibians and reptiles from the Late Pleistocene (MIS3) to present times, based on a comparative synthesis of the latest research published in recent years and the fossil record of the 58 archaeo-paleontological sites with significant assemblages. The paleoherpetofaunal associations make it possible to establish two major biotic regions during the Late Pleistocene. The first biotic region was located in the center and south of the Iberian Peninsula, with thermophilic species as the most representative taxa. The second biotic region was formed by the Atlantic-Cantabrian facade and the northeast Iberian area, dominated by hygrophilous and Euro-Siberian species, with an absence of Mediterranean species. After the Last Glacial Maximum there was an unprecedented concurrence in the northern Iberian Peninsula of autochthonous taxa from that area with thermophilic species. In the early Holocene, new species with no previous record in the Iberian Peninsula entered northern Iberia from eastern Mediterranean *refugia*. Finally, the introduction of North African species was the last significant biogeographical change during the Middle-Late Holocene.

1. Introduction

The last 60,000 years of the Quaternary have been characterized in Western Europe by major climatic and environmental changes as a result of the occurrence of the last great glacial pulsation and the beginning of the current warm interglacial. This time interval begins in MIS 3 (ca. 60,000 to 26,900 B.P.), alternating between phases of warming and cooling climate that correspond to the decline or increase of forests and semi-desert environments until the onset of MIS 2 (26,900 to 14,900 B.P.). At this point there occurs a major cooling process and a remarkable expansion of open arid spaces, with vegetation typical of cold and dry environments and with forest limited to areas of refuge (Fletcher and Sánchez-Goñi, 2008; Fletcher et al., 2010). MIS 1 (which starts at 14,900 B.P.) is characterized by a generalized warming of the climate, especially from the Holocene onwards (11,700 B.P.), and by a rapid increase in wooded areas. However, this phase also presents significant climatic fluctuations, though without outweighing the warm overall dynamic (Fletcher & Sánchez-Goñi, 2008; Fletcher et al., 2009; Walker et al., 2012; Naughton et al., 2015).

These large climatic and environmental changes have had a decisive impact on wildlife. The herpetofauna, reptiles and amphibians, is one of the animal groups that is most sensitive to temperature fluctuations due to the characteristic ectothermy of such organisms (Pough, 1980). This makes it a group of special interest for studying the effects that Quaternary climate changes have had on biodiversity (Araújo et al., 2008). All species of reptiles and amphibians in the Iberian fossil record of the Late Quaternary are currently represented in the Iberian Peninsula (Rage and Roček, 2002; Blain et al., 2011, 2014a, 2016). This facilitates actualist studies that allow us to observe the movements that have occurred

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in the geographical distribution of these groups leading to the current situation and to infer the possible paleoenvironmental and bioclimatic changes at a regional level (Blain, 2009).

To date, 51 species of reptiles and 28 species of amphibians have been described on the Iberian mainland, a herpetofaunal assemblage characterized by a great variability of thermal and ecological requirements (Masó and Pijoan, 2011). This includes typically Mediterranean taxa such as *Acanthodactylus erythrurus*, *Hemidactylus turcicus*, *Hemorrhois hippocrepis*, *Chamaeleo chamaeleon* and *Blanus cinereus*, and other species associated with Euro-Siberian climates such as *Lacerta agilis*, *Zootoca vivipara*, *Mesotriton* (*Ichthyosaura*) *alpestris* and *Rana temporaria*. The widespread mountainous terrain of the Iberian Peninsula has facilitated the emergence of species whose distribution is associated with high mountain climates, especially in northern Spain, examples being *Calotriton asper* and the genus *Iberolacerta* (Carretero et al., 2014). The high degree of knowledge currently available of the 79 herpetofaunal species with a current distribution in the Iberian Peninsula (Pleguezuelos et al., 2002; Masó and Pijoan, 2011; Salvador and Pleguezuelos, 2013; Carretero et al., 2014) results in a good bibliographical, biogeographical and statistical base for an analysis of the Iberian fossil herpetofauna. The biological requirements of each of these species generate particular restrictions that limit their biogeographical distribution and the viability of their populations, both at present and during the Quaternary, allowing us to infer the paleoclimate and the paleobiogeography by means of the fossil record (Blain et al., 2009a).

The phylogenies of different European species suggest the existence of a climatic refuge in the Iberian Peninsula through the successive glacial stages, from which these species would have subsequently repopulated the rest of the continent during the interglacial phases. This is a role similar to that played by the other peninsulas of southern Europe, the Balkans and Italy (Hewitt, 1996, 2000), made possible by the special climatic characteristics of their geographical location (Fletcher et al., 2010; Harrison and Sánchez-Goñi, 2010). In addition, the highly variable Iberian orography allowed the existence of a multitude of areas with different climatic and environmental characteristics, permitting the survival of species more adapted to temperate climates, in contrast to the situation in the rest of the continent (Nieto, 2011).

In the present study, by means of a comparative statistical analysis of the herpetofaunal associations from a total of 118 levels of 38 Iberian archaeo-paleontological sites in the Iberian Peninsula from the last 60,000 years (Fig. 1), we intend to identify the main changes in the distribution, composition and diversity of the reptiles and amphibians during the time interval analyzed. Our aim is to determine the main biogeographical movements of the different herpetofaunal species throughout the Iberian Peninsula and the role of the peninsula as a climate refuge during the Last Glacial Maximum and as a starting point for the subsequent recolonization of northern areas.

2. Material and methods

2.1. Data matrix

First, a bibliographical search has been carried out in the major journals of archaeology, paleontology and zooarchaeology, as well as a search through the major Internet search engines (mainly Google, Yahoo and Bing). For our statistical studies, the taxa identified in 118 levels of 38 paleo-archaeological sites chronologically dated to between early MIS 3 (*ca.* 60,000 B.P.) and the Bronze Age (*ca.* 3500 B.P.) have been compiled. These were then separated into three data matrices on the basis of biogeographical factors (Appendix A, B & C). For each level all the species present in the herpetological record have been included. In the case of genera with a single Iberian species (e.g., genus *Pelobates*), either currently or in the Quaternary fossil record (genus *Testudo*) (Morales and Sanchis, 2009), these have been assigned to the only species in question. The same goes for taxonomic identifications assigned to families that only have a single species present in the Iberian Peninsula (Geoemydidae or Emydidae). However, we have not included the genus-level citations of genera that have two or more species present in the Iberian Peninsula (e.g., genera *Bufo* sensu lato and *Natrix*).

In addition, we have applied some corrections to the data matrix to reduce dispersion and facilitate interpretation. The genus-level citations of the genera *Hyla*, *Lacerta* and *Vipera* from levels in the northern area have been included because of their biogeographical significance. For the same reason, the genus-level citations of *Pelodytes* and *Alytes* have also been included, despite the lack of species-level identification in some cases (e.g., Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013; Blain et al., 2013). Due to the problems in the paleontological literature of differentiating between *R. temporaria* and *Rana iberica* by osteological criteria (e.g., Zubeldia et al., 2007; Murelaga et al., 2011; Garcia-Ibaibarriaga et al., 2015), these two species have been grouped together as *R. temporaria-iberica* in the data matrix of the northern region. The citations of *Elaphe* sp., a snake genus that previously grouped together the current species *Zamenis scalaris* and *Zamenis longissimus*, have been assigned to *Z. scalaris* in the cases from Las Orcillas 1 and Lloma de Betxí, in accordance with the Iberian thermophilic tendencies of the herpetofaunal associations from their respective levels (Fernández et al., 2010; Tormo and De Pedro, 2013).

There are 20 levels with herpetofaunal record that have not been included in the matrix data. The chelonian citations from the paleo-archaeological sites of Gruta da Oliveira, Foz do Enxarrique, Abrigo de la Quebrada, Abric del Pastor, Cueva de San Luís, Cova Canet, Gruta do Escoural, Cova de l'Or, Ereta del Pedregal, Pic dels Corbs, Roca dels Bous, Cova del Gegant, Cova del Teixò, Can Sadurní, La Draga, Pont de Sadernes, El Pasteral, Cal Tintorer and Bòbila Madurell, as well as levels NV13, NM14 and NM4-2 of Cueva de Nerja (Jiménez Fuentes, 1986; Fernández Peris and Martínez Valle, 1989; Pérez Ripoll, 1990; Jiménez-Fuentes et al., 1998; Gómez and Jiménez Fuentes, 1998; Brugal and Raposo, 1999; Crespo, 2002; Mora et al., 2003; Budó et al., 2005; Félix et al., 2006; Morales and Sanchis, 2009; Aura et al., 2010; Jordá et al., 2011; Daura and Sanz, 2012; Sanchis et al., 2013, 2015; Pérez Ripoll, com. pers.), the citation of *Tarentola mauritanica* from level A.sup of Cova Colomera (López-García et al., 2010a), the citation of *R. iberica* from Cueva Millán (Esteban and Sanchiz, 1990) and the citation of *C. chamaeleon* from Cueva de Rincón de la Victoria (Talavera and Sanchiz, 1983) have been excluded from the northeastern and central-southern data matrices, to avoid statistical deviations owing to the large number of mono-specific citations without any other herpetofaunal taxa, although they are included in the subsequent discussion. Also, the citations of the genus *Testudo* that date from the Holocene of the northeastern area (Budó et al., 2005) have not been included because of the taxonomic revision they have undergone (Félix et al., 2006; Morales and Sanchis, 2009).

In order to compare the fossil record with the current situation, we have collected data on the present-day herpetofaunal assemblages from the same 10 × 10 km UTMs as the archaeo-paleontological sites included in the regional data matrices, through the "Especies por UTM" (species per UTM) function of the SIARE application website (Sistema de Información de Anfibios y Reptiles de España) (AHE, 2016).

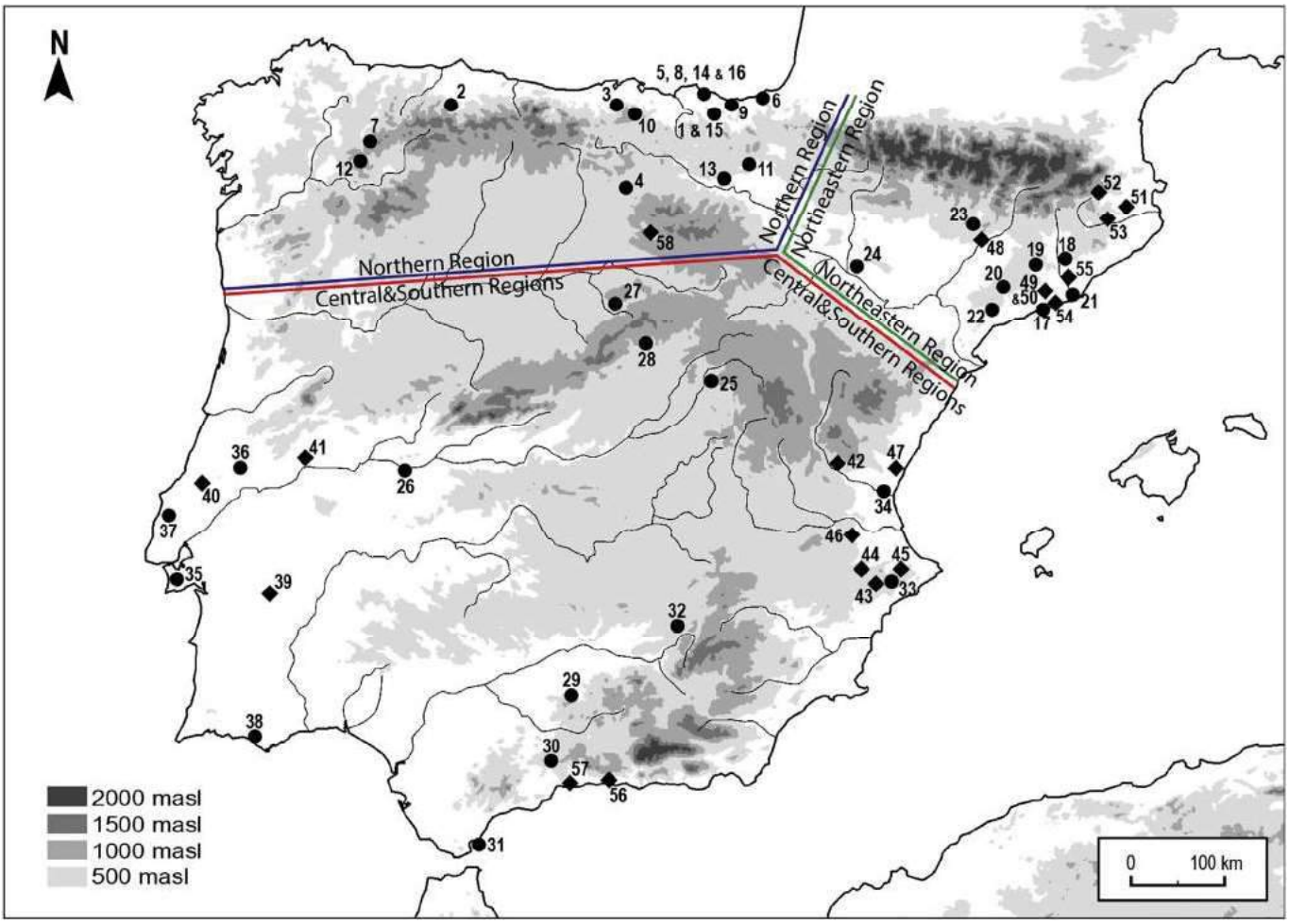

Fig. 1. Map with the latest Pleistocene-Late Holocene archaeo-paleontological sites mentioned in the text: 1) Askondo, 2) Cueva del Conde, 3) Cueva de Cobrante, 4) El Portalón, 5) Santimamiñe, 6) Erralla, 7) Valdavara-1, 8) Laminak II, 9) Aizkoltzo, 10) El Mirón, 11) Las Orcillas-1, 12) Cova Eirós, 13) Peña Larga, 14) Antoliñako Koba, 15) Dolmen of Errekatxuetako Atxa, 16) Santa Catalina, 17) Cova del Gegant, 18) Cova Teixoneres, 19) Abric Romaní, 20) Cova dels Xaragalls, 21) Riera de Canyars, 22) Cova dels Galls Carboners, 23) Cova Colomera, 24) Balsa la Tamariz, 25) Cueva de los Torrejones, 26) Sala de las Chimeneas of Maltravieso, 27) Peña de Estebanvela i, 28) Ventana, 29) Sima de Abraham, 30) Boquete de Zafarraya, 31) Gorham's Cave, 32) Castillejo del Bonete, 33) Abric del Salt, 34) Lloma de Betxí, 35) Gruta da Figueira Brava, 36) Gruta do Caldeirão, 37) Gruta Nova da Columbeira, 38) Guia of Albufeira, 39) Gruta do Escoural, 40) Gruta da Oliveira, 41) Foz do Enxarrique, 42) Abrigo de la Quebrada, 43) Abric del Pastor, 44) Cova Canet, 45) Cova de l'Or, 46) Ereta de Pedregal, 47) Pic dels Corbs, 48) Roca dels Bous, 49) Cova del Toixò, 50) Can Sadurní, 51) La Draga, 52) Pont de Sadernes, 53) El Pasteral, 54) Cal Tintorer, 55) Bòbila Madurell, 56) Cueva de Nerja, 57) Cueva de Rincón de la Victoria and 58) Cueva Millán. The sites marked with a circle are those included in the regional data matrices, while those marked with a rhombus have been excluded from them.

2.2. Classification of levels

The 118 levels have been grouped, in accordance with the geographical situation of the 38 different paleo-archaeological sites (Fig. 1; Table 1), into three data matrices (Appendix A, B & C). In each data matrix, species with a regional fossil record have been grouped into the rows, while the archaeo-paleontological levels, with their corresponding taxonomic lists, have been grouped into the columns. Therefore, in the binary data base the presence of a taxon is marked by "1" and its absence by "0". The three resultant data matrices are:

Northern Region: this includes 16 sites located between Galicia and Navarra, covering the entire Cantabrian fringe and inner area as far as Portalón de Atapuerca at its southern boundary. This region is currently characterized by a humid climate due to the Atlantic influence, with rather cold winters and temperate summers. Overall, there is a good distribution of levels throughout the studied period and all the archaeological cultures known for this region are represented: the Mousterian associated with *Homo neanderthalensis* and the Aurignacian, Gravettian, Solutrean, Magdalenian, Azilian, Microlaminar Epipaleolithic, Mesolithic, Neolithic, Chalcolithic and Bronze Age that are linked to Anatomically Modern Man. A total of 75 archaeo-paleontological levels (Table 1) and 24 different taxa have been included in the data matrix for the northern region (Appendix A).

Northeastern Region: this includes 8 sites located in present-day Catalonia and Aragon, from the Mediterranean to the Pyrenees and the Middle Ebro River Valley, in the northern area of the Mediterranean side of Iberia. Most of these sites are dated to MIS 3 while most of the MIS 1 records are mono-specific chelonian citations, which have not been included in the data matrix. At present, there are no sites in this area with published herpetofauna dated to MIS 2. The human cultures represented in the total of 23 archaeological levels (Table 1) are Mousterian, Neolithic and Bronze Age and 17 different herpetofaunal taxa have been included in the data matrix for the northeastern zone (Appendix B).

Central and Southern Regions: this group includes 14 sites in the Mediterranean area, mainly distributed in Castilian and Extremaduran areas, Andalusia, central and southern Portugal, and the center of the Valencia Country. The human cultures represented in

Table 1
- List of the latest Pleistocene-Late Holocene archae-paleontological sites and levels included in the regional data matrices. Regions: *N*, Northern region; *NE*, Northeastern region; *C&S*, Central and Southern regions.

Sites	Levels	Region	References
1. Askondo	13, 9, 8, 7, 6, 5, 3, 2 & 1	N	Garete and Rios-Garaizar, 2011; Garcia-Ibaibarriaga et al., 2015
2. Cueva del Conde	N104, N103, N10b, N20a, N2a1 & N2a2	N	Arbizu et al., 2005; López-García et al., 2011c
3. Cobrante	N7 to N1	N	Rasines, 2009; Martín et al., 2009
4. Portalón de Atapuerca	P16 to P1	N	Carretero et al., 2008; Ruíz-Zapata et al., 2008; López-García et al., 2010b
5. Cova Eirós	3 & 2	N	Rey-Rodríguez et al., 2016
6. Antoliñako Koba	D, C, B & A	N	Zubeldia et al., 2007
7. Santimamiñe	Arg-o, Camr, Csn, Balm, Almp, Slnc, Arcp, Slm & Lsm	N	Murelaga et al., 2011; Rofes et al., 2014
8. Erralla	VI, V, IV, III & II	N	Esteban and Sanchiz 1985; Peman 1985; Altuna 1985
9. Valdavara-1	Lower & Upper Units	N	Vaquero et al., 2009; Blain et al., 2009b; López-García et al., 2011b
10. Santa Catalina	III, II & I	N	Arribas and Berganza, 2010; Bailon and García-Ibaibarriaga, 2014
11. Laminak II	II-I	N	Arribas and Berganza, 1989; Sanchiz and Esteban 1994; Peman, 1994; Berganza and Arribas, 1994
12. Aizkoltzo	L.15-12	N	Murelaga et al., 2008
13. El Mirón	10 to 3	N	Straus et al., 2001; Sanchiz et al., 2012
14. Las Orcillas-1	C.II-I	N	Fernández et al., 2010
15. Peña Larga	IV-I	N	Castaños 1997; Murelaga et al., 2009; Rofes et al., 2013
16. Errekatxuetako Atxa's Dolmen	Bell Beaker level	N	Murelaga et al., 2007
17. Teixoneres	IIb & II	NE	Tissoux et al., 2006; Rosell et al., 2010, 2014; López-García et al., 2012b, 2014a
18. Cova del Gegant	V, IV & III	NE	Daura et al., 2005, 2010; Daura and Sanz, 2012; López-García et al., 2007, 2008, 2012a, 2014a
19. Abric Romaní	O, K, J, E & D	NE	Burjachs and Julià, 1994; Burjachs et al., 2012; López-García et al., 2014a
20. Xaragalls	C8 to C3	NE	López-García et al., 2012c
21. Terrassa de la Riera dels Canyars	Fluvial deposit	NE	Daura et al., 2013; López-García et al., 2013, 2014a
22. Galls Carboners	L.108-105	NE	López-García et al., 2014b
23. Cova Colomera	C15, C14–15, C12 & EE1	NE	Oms et al., 2009; López-García et al., 2010a
24. Balsa la Tamariz	Burial sites and prehistoric settlement	NE	Royo and Rey, 1993; Rey and Royo, 1993; Laplana and Cuenca-Bescós, 1995
25. Cueva de los Torrejones	L.5-4	C&S	Arribas et al., 1995, 1997
26. Sala de las Chimeneas, Maltravieso	A	C&S	Rodríguez et al., 2009; Bañuls-Cardona et al., 2012
27. Peña de Estebanvela	VI, IV, III, II & I	C&S	Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013; Cacho et al., 2013
28. Cueva de la Ventana	Units 7-9-16-22-26, 14-18-26 & 3-4	C&S	Sánchez Marco et al., 2005
29. Sima de Abraham	Deposit 11	C&S	Martínez-Sánchez et al., 2010, 2012
30. Boquete de Zafarraya	Unit Id-Ia	C&S	Barroso and Bailon, 2003; Barroso et al., 2003; Zilhao, 2006
31. Gorham's Cave	IV, IIIb & IIIa	C&S	Gleed-Owen, 2001; Finlayson et al., 2006; Jennings et al., 2011; López-García et al., 2011a; Blain et al., 2013
32. Castillejo del Bonete	Sedimentary filling of the burial tumulus	C&S	Benítez de Lugo et al., 2016
33. Cova del Salt	XI	C&S	Pérez Luís, 2014
34. Lloma de Betxí	Bronze Age settlement	C&S	De Pedro, 2004; Tormo and De Pedro, 2013
35. Gruta da Figueira Brava	Mousterian sequence	C&S	Crespo et al., 2000; Lapparent de Broin and Antunes, 2000; Crespo, 2002
36. Gruta do Caldeirão	Mousterian sequence	C&S	Crespo, 2002
37. Gruta Nova da Columbeira	Mousterian sequence	C&S	Jiménez Fuentes et al., 1998; Crespo, 2002
38. Guia de Albufeira	Postglacial pleistocenic sequence	C&S	Crespo, 2002

the 22 archaeological levels (Table 1) are the Mousterian, Solutrean, Magdalenian, Epipaleolithic, Neolithic, the Motillas Culture and the Valencian Bronze Culture. In the data matrix for these areas 29 different taxa have been included (Appendix C).

2.3. Statistical methodology

The method of hierarchical clustering has been chosen to perform the statistical analysis, because this generates a dendrogram that reveals the relationships of similarity and difference between the species concurring in the archaeo-paleontological levels included in the data matrices. The aim is to infer whether or not the resulting herpetofaunal groups are based on chronostratigraphic criteria whose origins are related to possible biogeographic changes. In addition, the Jaccard similarity index has been applied, since this is recommended for clustering binary data, because it gives more importance to joint occurrences in the assemblages (Hammer et al., 2001). Also, the "unweighted pair-group average" has been applied to the three data matrices, resulting in the union in the dendrogram of different groups based on the average distance between their members.

Moreover, a correspondence analysis (CA) has been used to support the results of the hierarchical clustering. The CA is the recommended method for comparing associations (assigned to columns) with the total count of taxa, or identifying taxa (assigned to rows) through the associations (Greenacre, 2010). In the case of this paper its aim is to mark the relationships of proximity between taxa of different associations, grouping them closely in contrast to the more atypical taxa, which will appear in an eccentric position in relation to the rest of the set. The Paleontological Statistics program (PAST3) has been used for all statistical approaches (Hammer et al., 2001).

3. Results

A preliminary analysis of the data matrices shows clear differences in the typical composition of the three analyzed areas. For the prehistoric sequence of the northern region the most representative species are *R. temporaria* (or *R. temporaria-iberica*) (present in 69 assemblages, 90.8% of the total), *Anguis fragilis* (35 assemblages, 46.1%), *Bufo spinosus* (32 assemblages, 42.1%) and to a lesser extent *Bufo calamita* (29 assemblages, 38.1%), the genus *Alytes* (27

assemblages, 35.5%) and the genus *Vipera* (19 assemblages, 25%) (Appendix A), forming a typical association of forest environments and wet meadows. For the northeastern Iberian area the most significant taxa are *B. calamita* (13 assemblages, 56.5%), *R. temporaria* (12 assemblages, 52.2%), *Alytes obstetricans* (11 assemblages, 47.8%) and *A. fragilis* (10 assemblages, 43.5%) and to a lesser extent *B. spinosus* (9 assemblages, 39.1%), *Coronella girondica* (8 assemblages, 34.8%) and *Pelodytes punctatus* (8 assemblages, 34.78%) (Appendix B), which form a herpetofaunal association with a marked preference for humid environments and high rainfall, with the exception of *C. girondica*.

Both zones located in the northern third of the Iberian Peninsula share a herpetofauna with hygrophilous tendencies and a predilection for humid environments. However, the prevalence of *B. calamita* at the expense of *R. temporaria* in the northeastern region, coupled with the significant presence of *P. punctatus* and *C. girondica*, can be related to the greater influence of Mediterranean environments, correlated with its geographical position in the Western Mediterranean basin.

In contrast, a Mediterranean influence and thermophilic tendencies become more evident in the herpetofaunal fossil record of the remaining two thirds of the Iberian Peninsula, comprising the central, eastern and southern areas. In these regions the predominant species are *B. calamita* (15 assemblages, 68.2%), *Timon lepidus* (14 assemblages, 63.6%), *B. spinosus* (11 assemblages, 50%), *Z. scalaris* (10 assemblages, 45.4%) and in lesser measure *Pelobates cultripes* (8 assemblages, 36.4%), *Testudo hermanni* (8 assemblages, 36.4%), *Malpolon monspessulanus* (7 assemblages, 31.8%), *Pleurodeles waltl* (6 assemblages, 27.3%) and *Vipera latastei* (6 assemblages, 27.3%) (Appendix C). Together, these species are a typical association in current Mediterranean dry environments with a water regime that is markedly seasonal and the presence of open environments, scrubs and forests.

Application of the statistical analysis methods CA and hierarchical clustering to the three data matrices shows remarkable and consistent trends between the two methods. In the northern region the resulting cluster distinguishes three groups (Fig. 2A). The first group is formed by the species *B. calamita*, *B. spinosus*, *R. temporaria-iberica*, *A. fragilis* and the genera *Alytes* and *Vipera*, an association of generalist herpetofauna that is tolerant to Euro-Siberian conditions. In addition, these taxa are the only ones present in the fossil record of the Cantabrian fringe during MIS 2, the last glacial phase, and they are almost exclusive during MIS 3. The second cluster group is composed of the species *Coronella austriaca*, *Natrix maura*, *Chalcides striatus*, *I. alpestris*, *C. girondica*, *Hierophis viridiflavus*, *Lissotriton helveticus*, *Natrix natrix*, *Z. longissimus*, *Salamandra salamandra* and the genera *Hyla* and *Lacerta*. With the exception of *S. salamandra*, which has a fossil record from Cueva del Conde in MIS 3 (López-García et al., 2011c), all are hygrophilous and/or generalist taxa, tolerant to a Euro-Siberian influence, which appear in the regional fossil record during MIS 1, i.e. during the last postglacial and interglacial stages. Finally, the third group in the regional cluster is formed by *Chioglossa lusitanica*, *Discoglossus galganoi*, *T. lepidus*, *Z. scalaris* and *M. monspessulanus*. These five species also appear in the fossil record of the Iberian North during MIS 1. Except for *C. lusitanica*, which is a salamander endemic to the northwestern Iberian region (Vences, 2002), the remaining taxa are thermophilic species linked to the Mediterranean influence. This is due to the presence of the unique fossil record of *C. lusitanica* in the herpetofaunal assemblage of the Upper Unit of Valdavara-1, where also appears another thermophilic herpetofauna as *D.* cf. *galganoi*, *T. lepidus* and *M. monspessulanus* (Blain et al., 2009b; López-García et al., 2011b).

The same overview is obtained by CA, the same three groups appearing in the graphical representation of CA (Fig. 2B). The species present in the northern assemblages in MIS 3 and MIS 2 have been grouped in the right half of the graph. *S. salamandra*, absent in MIS 2 but present in MIS 3, appears in the graph in a slightly eccentric position relative to the rest of the group of hygrophilous and/or generalist species of MIS 1, but it is not grouped together with the taxa of the glacial phase, which are located in the right third of the graph.

For the northeastern Iberian region the same scenario as in the northern zone is partially repeated, although the lack of a herpetofaunal record for MIS 2 rules out any further comparison between these two Iberian regions. In the northeastern cluster the tripartite scheme is repeated (Fig. 3A). The first group is formed by *P. cultripes*, *T. lepidus*, *Z. scalaris* and *M. monspessulanus*, thermophilic species of Mediterranean influence that appear in the regional record in MIS 1, even though *P. cultripes* has a previous record in MIS 3 (López-García et al., 2012a). The second group is formed by the species that occur in the fossil record of this region for MIS 3: *S. salamandra*, *A. obstetricans*, *P. punctatus*, *B. calamita*, *B. spinosus*, *R. temporaria*, *A. fragilis*, *C. austriaca*, *C. girondica*, *Vipera aspis* and *V. latastei*. The third group is composed of *N. maura* and *C. asper*, which appear in the regional record in MIS 1. *N. maura* is a water snake with generalist trends, while *C. asper* is a newt endemic to the Pyrenees Mountains. Applying CA to the same data matrix shows a clear separation of thermophilic Mediterranean species with respect to the other taxa. It also shows a position near the binomial *C. asper* and *N. maura* for the conjunction of species from MIS 3, though separated from them, in correlation with the hygrophilous, tolerant tendencies of both groups (Fig. 3B).

Finally, for the central-southern quadrants of the Iberian Peninsula, the dendrogram is much less clear compared to the previous two. In this case the different groups do not correspond to chronological criteria, suggesting possible stability in the composition of the herpetofaunal fossil record of this region, which is entirely composed of typical Iberian Mediterranean species (Fig. 4.A). However, the existence of potential biases in the fossil record and/or data matrix cannot be ruled out. These could be indicated in the cluster by the position of the three chelonian species, which are only represented in the data matrix by citations in assemblages in archaeo-paleontological levels, although the quantity of mono-specific citations is higher in the literature. Nonetheless, if these three taxa are excluded, the scenario expounded by the CA allows the existence of a single large group of taxa to be distinguished. The exceptions are the species *S. salamandra* and *Psammodromus algirus* and the genus *Alytes* because of their eccentric positions relative to the other taxa, though they orbit around the main group (Fig. 4.B). In the case of *P. algirus*, which is an abundant species in the Mediterranean bioregion, this is possibly due to the difficulty of documenting its presence in the fossil record because of the problems in identifying the diagnostic osteological characters, resulting in a small number of citations in the assemblages. In the cases of *S. salamandra* and *Alytes* this may be due to their more hygrophilous tendencies in contrast to the rest of the taxa in the region, which provides a dry and thermophilic context that is in principle less suitable for these amphibians.

Comparing the data with the current situation, in the total of 14 10 × 10 km UTMs where the archaeo-paleontological sites included in the data matrix of the northern region are located, the following species are present: *B. spinosus* (14 assemblages, 100% of the total); *A. fragilis* and *A. obstetricans* (13 assemblages, 92.8%); *L. helveticus* and *N. maura* (12 assemblages, 85.7%); *Pelophylax perezi*, *Podarcis liolepis* and *S. salamandra* (11 assemblages, 78.6%); *Lacerta bilineata*, *N. astreptophora*, *Podarcis muralis*, *R. temporaria* and *Vipera seoanei* (10 assemblages, 71.4%); *Triturus marmoratus* (9 assemblages, 64.3%); *C. striatus*, *Lacerta schreiberi* and *Z. vivipara* (8 assemblages,

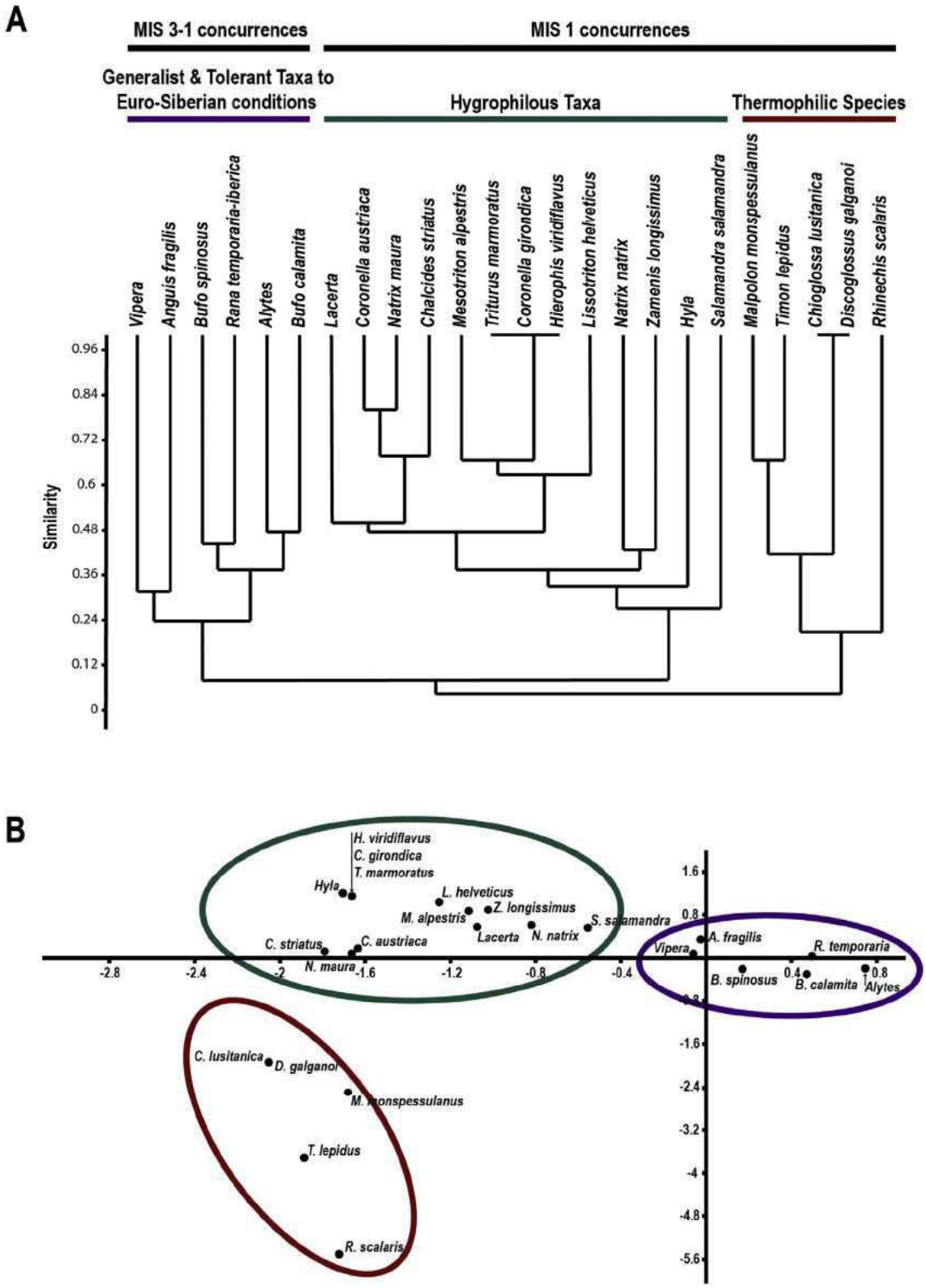

Fig. 2. - Northern Iberian herpetofaunal record: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the correspondence analysis of latest Pleistocene-Late Holocene assemblages.

57.1%); *C. austriaca* (7 assemblages, 50%); *C. girondica* and *R. iberica* (6 assemblages, 42.8%); *Z. longissimus* and *T. lepidus* (5 assemblages, 35.7%); *B. calamita*, *D. galganoi*, *Hyla molleri* and *I. alpestris* (4 assemblages, 28.6%); *Mauremys leprosa* and *Z. scalaris* (3 assemblages, 21.4%); *Iberolacerta monticola*, *Lissotriton boscai*, *M. monspessulanus*, *P. punctatus*, *Podarcis bocagei*, *P. algirus* and

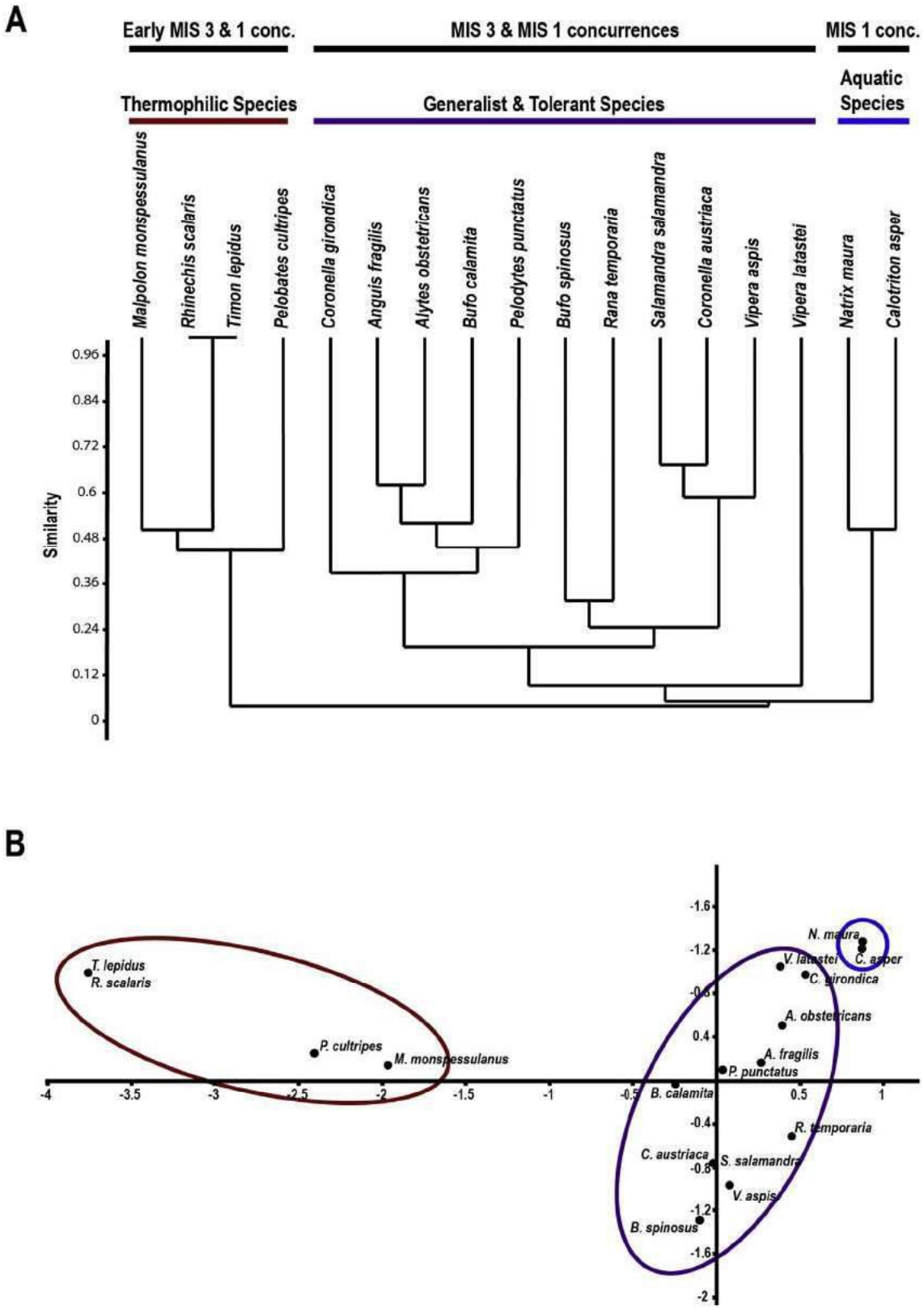

Fig. 3. - Northeastern Iberian herpetofaunal record: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the correspondence analysis (C) of latest Pleistocene-Late Holocene assemblages.

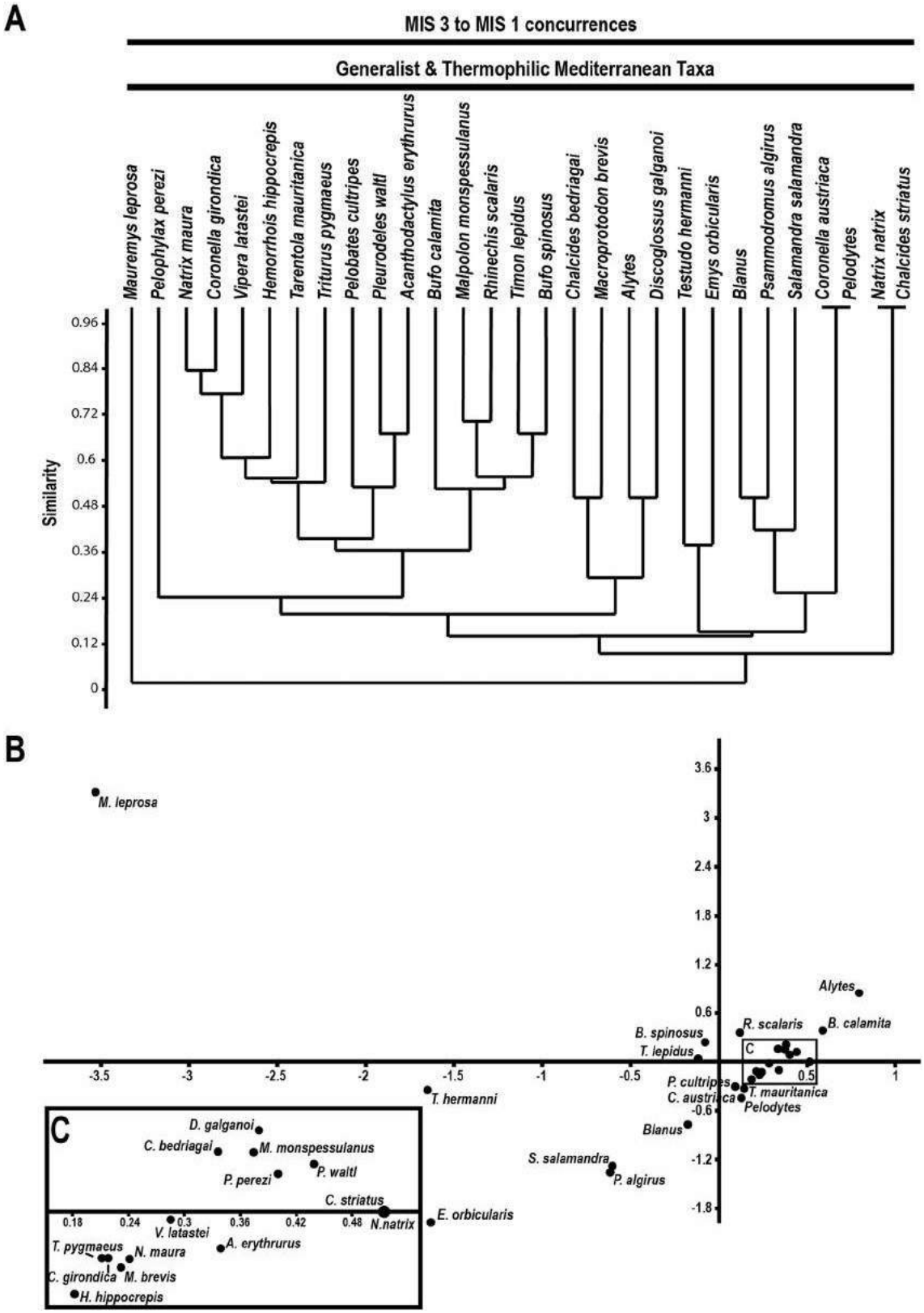

Fig. 4. - Central and southern Iberian fossil records: A) dendrogram of the cluster analysis with the Jaccard similarity index, and B) graphical representation of the correspondence analysis, with enlarged detail (C), of the latest Pleistocene-Late Holocene assemblages.

V. aspis (2 assemblages, 14.3%); *B. cinereus*, *C. lusitanica*, *Emys orbicularis*, *Rana dalmatina* and *V. latastei* (1 assemblage, 7.1%) (Table 2) (based on AHE, 2016).

At present, at a specific level, *Z. vivipara*, the different species of the genus *Podarcis*, *P. algirus*, *H. molleri*, *E. orbicularis*, *M. leprosa*, *B. cinereus*, *V. aspis*, *V. latastei*, *L. boscai*, *P. punctatus*, *P. perezi*, *L. bilineata*, *L. schreiberi* and *I. monticola* have no fossil record in the latest Quaternary in the Cantabrian region. By contrast with its absence in the fossil record, *P. perezi* is notable for its high presence in the current assemblages, although the available genetic studies have not suggested applicable paleobiogeographical scenarios for the region studied here (Hotz et al., 1994; Arano et al., 1995; Montori, 2014).

In the northeastern region the current situation is very different from the latest Quaternary herpetofauna as known until now, especially for MIS 3. Thus, in the 8 current assemblages located in the same 10 × 10 km UTMs as the sites included in the northeastern area of the Iberian Peninsula, the following species are present: *B. calamita*, *B. spinosus*, *M. monspessulanus*, *P. perezi*, *P. liolepis*, *P. algirus* and *T. lepidus* (8 assemblages, 100%); *A. obstetricans*, *N. maura*, *Z. scalaris*, *S. salamandra* and *T. mauritanica* (7 assemblages, 87.5%); *C. girondica*, *N. astreptophora* and *P. punctatus* (6 assemblages, 75%); *A. fragilis* and *V. latastei* (5 assemblages, 62.5%); *Hyla meridionalis*, *M. leprosa*, *P. cultripes* and *Psammodromus*

Table 2
Comparison between latest Pleistocene-Late Holocene (MIS3-MIS1) and present-day herpetofaunal assemblages from the same 10 × 10 km UTMs as the archaeo-paleontological sites included in the regional data matrices.

	Northern region		Northeastern region		Central & Southern regions	
	MIS 3 – MIS 1	Today	MIS 3 – MIS 1	Today	MIS 3 – MIS 1	Today
≥ 75% to 100%	*R. temporaria-iberica*	*A. obstetricans* *A. fragilis* *B. spinosus* *L. helveticus* *N. maura* *P. perezi* *P. liolepis* *S. salamandra*		*A. obstetricans* *B. calamita* *B. spinosus* *C. girondica* *M. monspessulanus* *N. maura* *P. perezi* *P. waltl* *P. algirus* *Z. scalaris* *T. mauritanica* *T. lepidus*		*B. calamita* *B. spinosus* *M. monspessulanus* *N. maura* *N. astreptophora* *P. punctatus* *P. perezi* *P. liolepis* *P. algirus* *Z. scalaris* *S. salamandra* *T. mauritanica* *T. lepidus* *V. latastei*
≥ 50% to < 75%		*C. striatus* *C. austriaca* *L. bilineata* *L. schreiberi* *N. astreptophora* *P. muralis* *R. temporaria* *T. marmoratus* *V. seoanei* *Z. vivipara*	*B. calamita* *R. temporaria*	*A. fragilis* *H. meridionalis* *M. leprosa* *P. cultripes* *P. edwardsianus* *V. latastei*	*B. calamita* *B. spinosus* *T. lepidus*	*C. girondica* *H. hippocrepis* *M. leprosa* *N. astreptophora* *P. cultripes* P. *hispanicus*
≥ 25% to < 50%	*Alytes* *A. fragilis* *B. spinosus* *B. calamita* *Vipera*	*B. calamita* *C. girondica* *D. galganoi* *H. molleri* *I. alpestris* *R. iberica* *T. lepidus* *Z. longissimus*	*A. obstetricans* *A. fragilis* *B. spinosus* *C. girondica* *P. punctatus*	*C. striatus* *H. turcicus* *H. hippocrepis* *P. muralis*	*M. monspessulanus* *P. cultripes* *P. waltl* *Z. scalaris* *T. hermanni* *V. latastei*	*A. obstetricans* *B. cinereus* *C. bedriagai* *C. striatus* *D. galganoi* *H. turcicus* *H. meridionali* *H. molleri* *P. guadarramae* *T. pygmaeus*
< 25%	*C. striatus* *C. lusitanica* *C. austriaca* *C. girondica* *D. galganoi* *H. viridiflavus* *Hyla* *Lacerta* *L. helveticus* *M. monspessulanus* *I. alpestris* *N. maura* *N. natrix* s.l. *Z. scalaris* *S. salamandra* *T. lepidus* *T. marmoratus* *Z. longissimus*	*B. cinereus* *C. lusitanica* *E. orbicularis* *I. montícola* *L. boscai* *M. monspessulanus* *M. leprosa* *P. punctatus* *P. bocagei* *P. algirus* *R. dalmatina* *Z. scalaris* *V. aspis* *V. latastei*	*C. asper* *C. austriaca* *M. monspessulanus* *N. maura* *P. cultripes* *Z. scalaris* *S. salamandra* *T. lepidus* *V. aspis* *V. latastei*	*D. pictus* *L. helveticus* *T. marmoratus* *V. aspis* *Z. longissimus*	*A. erythrurus* *Alytes* *Blanus* *C. bedriagai* *C. striatus* *C. austriaca* *C. girondica* *D. galganoi* *E. orbicularis* *H. hippocrepis* *M. brevis* *M. leprosa* *Natrix maura* *N. natrix* s.l. *Pelodytes* *P. perezi* *P. algirus* *S. salamandra* *T. mauritanica* *T. pygmaeus*	*A. erythrurus,* *A. cisternasii* *A. dickhilleni* *C. chamaeleon* *E. orbicularis* *L. schreiberi* *L. boscai* *M. brevis* *P. ibericus* *P. punctatus* *P. hispanica* *P. vaucheri* *P. virescens* *P. edwardsianus* *S. salamandra* *T. marmoratus*

edwardsianus (4 assemblages, 50%); *C. striatus* (3 assemblages, 37.5%); *H. turcicus*, *H. hippocrepis* and *P. muralis* (2 assemblages, 25%); *Discoglossus pictus*, *L. helveticus*, *T. marmoratus*, *V. aspis* and *Z. longissimus* (1 assemblage, 12.5%) (Table 2) (AHE, 2016). *P. perezi*, *P. liolepis*, *P. algirus*, *Z. scalaris*, *H. meridionalis*, *P. edwardsianus*, *H. turcicus*, *H. hippocrepis*, *P. muralis*, *D. pictus*, *L. helveticus*, *T. marmoratus* and *Z. longissimus* are species absent from the prehistoric record of the Late Quaternary in the northeastern Iberian area. The turtles *T. hermanni*, *M. leprosa* and *E. orbicularis* have a fossil record in northeastern Iberia during the latest Pleistocene and Holocene, although they are mono-specific citations that have been excluded from the regional data matrix (Mora et al., 2003; Budó et al., 2005; Félix et al., 2006; Morales and Sanchis, 2009; Daura and Sanz, 2012).

For the southern and central regions, the following species are present in the nine current assemblages located in the same 10 × 10 km UTMs as the sites included within the limits of the Spanish State: *B. calamita*, *B. spinosus*, *N. maura*, *P. perezi*, *P. algirus*, *Z. scalaris* and *T. lepidus* (9 assemblages, 100%); *M. monspessulanus* and *T. mauritanica* (8 assemblages, 88.89%); *P. waltl* and *V. latastei* (7 assemblages, 77.78%); *C. girondica*, *H. hippocrepis*, *M. leprosa*, *N. astreptophora* and *P. cultripes* (6 assemblages, 66.67%); *Psammodromus hispanicus* (5 assemblages, 55.55%); *B. cinereus*, *Chalcides bedriagai*, *D. galganoi*, *H. turcicus* and *H. molleri* (4 assemblages, 44.44%); *A. obstetricans*, *C. striatus*, *H. meridionalis*, *Podarcis guadarramae* and *Triturus pygmaeus* (3 assemblages, 33.33%); *A. erythrurus*, *E. orbicularis*, *L. schreiberi*, *Macroprotodon brevis*, *Pelodytes ibericus*, *P. punctatus*, *Podarcis hispanica*, *Podarcis vaucheri*, *Podarcis virescens*, *P. edwardsianus*, *S. salamandra* and *T. marmoratus* (2 assemblages, 22.22%); *Alytes cisternasii*, *Alytes dickhilleni*, *C. chamaeleon* and *L. boscai* (1 assemblage, 11.11%) (Table 2) (AHE, 2016).

The different species of the genera *Podarcis* and *Hyla*, as well as the species *A. dickhilleni*, *A. obstetricans*, *H. turcicus*, *L. schreiberi*, *L. boscai*, *P. ibericus*, *P. edwardsianus*, *P. hispanicus* and *T. marmoratus*, are without citations at a specific level in the central-southern fossil record for the period between MIS 3 and MIS 1.

4. Discussion

4.1. Cantabrian northern region

The most representative taxa for the prehistoric sequence of the end of the Upper Pleistocene and Holocene in the northern Iberian area, which ranges from Navarre to Galicia, are *B. spinosus*, *B. calamita*, *R. temporaria* (or *R. temporaria-iberica*), *A. fragilis* and the genera *Alytes* and *Vipera*, which are a typical assemblage in forest environments and wet meadows with abundant water points.

A. fragilis is a legless lizard widely distributed across Euro-Siberian Europe, which extends significantly into the northern portion of the Iberian Peninsula. It is a hygrophilous species that occupies a wide range of habitats typical of the Euro-Siberian region, especially those with a dense herbaceous stratum, although it may occasionally appear in the supra-Mediterranean and oro-Mediterranean bioclimatic levels of the Iberian Mediterranean area (Galán and Salvador, 2009), provided that the average annual rainfall exceeds 600 mm (Llorente et al., 1995). Also, its presence is negatively correlated with the number of annual hours of sunshine and with the average temperature of the warmest month, for it prefers cooler and wetter areas with the rainfall distributed throughout the year (Smith, 1998). *B. spinosus* currently prefers the forested areas of the northern Iberian area, deciduous forests with the presence of water courses and, to a lesser extent, wet meadows (Ortiz-Santaliestra, 2014). *R. temporaria* limits its distribution range to areas with temporary or permanent water points (Álvarez, 2014) and it depends on an average annual rainfall that exceeds 1100 mm in the eastern Cantabrian area (Gosá and Bergerandi, 1994).

The documented assemblages dating from MIS 3 and MIS 2 in northern Iberia stand out for the low variety of identified taxa: *S. salamandra*, *A. obstetricans*, *B. calamita*, *B. spinosus*, *R. temporaria-iberica*, *A. fragilis* and *Vipera* sp. (Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b, 2011c; Garcia-Ibaibarriaga et al., 2015), in addition to the citations of Ophidia indet. (López-García et al., 2010b), Colubrinae indet. (Martín et al., 2009) and Salamandridae indet. (Zubeldia et al., 2007). Compared to MIS 3, the fossil record of MIS 2 is thus notable for the absence of fossil remains from Salamandridae and Colubridae, as well as the presence of a single record of the genus *Vipera* in the fossil record for the northern area (López-García et al., 2010b). *A. fragilis*, which is widely represented in the sequences of MIS 3 and MIS 1, is only found in level Arg-o of Santimamiñe (Murelaga et al., 2011) and level C of Antoliñako Koba (Zubeldia et al., 2007). The typical association is reduced to *A. obstetricans*, *B. calamita*, *B. spinosus* and *R. temporaria-iberica* (Esteban and Sanchiz, 1985; Zubeldia et al., 2007; Martín et al., 2009; López-García et al., 2010b; Murelaga et al., 2011), with sporadic records of *A. fragilis* (Zubeldia et al., 2007; Murelaga et al., 2011), *Vipera* sp. (López-García et al., 2010b), Lacertidae indet. (cf. *Podarcis*) (Zubeldia et al., 2007; López-García et al., 2010b) and the probable *R. dalmatina* from Erralla VI (Esteban and Sanchiz, 1985).

The species present before and during the Last Glacial Maximum are mostly generalist species that can tolerate a wide climatic and environmental spectrum (*B. spinosus*, *B. calamita*, *A. fragilis* and the genera *Rana* and *Vipera*). Significantly, the northern sequence is monopolized by *R. temporaria*, a species that has a pronounced preference for humid environments and Euro-Siberian climatic conditions, and this frog species appears in all of the documented assemblages in the sequences of MIS 3 and MIS 2.

In the fossil record, significant changes are detected in the composition of herpetofaunal associations from the beginning of MIS 1. In some assemblages the number of hygrophilous and generalist species increases, while species linked to a Mediterranean influence appear in this area for the first time. The first citation of a thermophilic species in the fossil record of northern Iberia during the postglacial period is the snake *M. monspessulanus* in the Lower Unit of Valdavara-1 (15,120 ± 70 B.P.-13,770 ± 70 B.P, Vaquero et al., 2009; López-García et al., 2011b). These absolute datings situate the Lower Unit of Valdavara-1 in the warm climate phase of the Bölling-Allerød interstadial (Naughton et al., 2015) and are consistent with the presence of *M. monspessulanus*. This is a fully thermophilic snake with high thermal requirements (Cheylan et al., 1981; Blázquez and Pleguezuelos, 2002), whose appearance in the Galician area can be related to a process of colonization of the northern region from a southern Iberian *refugium* due to the rising temperatures after the end of MIS 2.

The latest Pleistocene sequence in the Lower Unit of Valdavara-1 also features the first appearance of the snakes *N. maura*, *N. natrix* (sensu lato) and *C.* cf. *austriaca* and the reappearance of *S. salamandra*, which is absent in MIS 2. Further, in this same unit the genus *Lacerta* (sensu lato) is cited for the first time in the regional record of the Late Pleistocene (López-García et al., 2011b). This is an interesting citation given that Lacerta sensu lato in the northern area includes three diferent species (*T. lepidus*, *L. schreiberi* and *L. bilineata*), which underwent three different processes of postglacial colonization according to molecular data from the Cantabrian fringe (Paulo et al., 2001, 2002a; Guedes, 2015). Therefore, greater efforts or news sub-fossil discoveries are required for their species-level assignment.

In the eastern part of the Cantabrian fringe, in the Basque

Country, the three levels with herpetofaunal assemblages from Cueva de Santa Catalina, and especially levels N.II and N.I, stand out for the high diversity of their assemblages in the early Pre-Boreal stage of the Holocene (Bailon and García-Ibaibarriaga, 2014). The newt cf. *I. alpestris* has its first record in level N.III in the final phase of the latest Pleistocene (between 12,425 ± 90 B.P. and 12,345 ± 85 B.P.), while in the Holocene level N.II (11,155 ± 80 B.P.) and level N.I (between 10,530 ± 110 B.P. and 9180 ± 110 B.P.) (Arribas and Berganza, 2010) some species previously absent from the prehistoric sequence of the Late Pleistocene appear in concurrence: cf. *L. helveticus*, *Triturus* cf. *marmoratus*, *C. striatus*, *C.* cf. *girondica*, cf. *Z. longissimus* and cf. *H. viridiflavus*. *Lacerta* sp. (= *Lacerta* sensu lato) also appears in both Holocene levels from Santa Catalina, with the same taxonomic problems as in the aforementioned case of the Lower Unit of Valdavara-1. The frog *Hyla* sp., an unprecedented genus in the regional record, appears in level N.II of Santa Catalina (Bailon and García-Ibaibarriaga, 2014).

Levels N.II and N.I of Santa Catalina provide two rich assemblages of species that currently have diverse biogeographical dynamics, which might suggest multiple colonizations in the Cantabrian area from distant and different *refugia*. However, the case of *L. helveticus* invokes caution with respect to these hypotheses. This newt is distributed from the northern third of the Iberian Peninsula to the northern tip of Great Britain and the extreme west of the Czech Republic (Schlüpmann and van Gelder, 2004). Molecular analyses have identified great genetic diversity among its Iberian populations, which are grouped into four different clades. It was exclusively the eastern clade of *L. helveticus* that carried out the postglacial colonization of Western and Central Europe, the Iberian Peninsula thus serving as its glacial refuge (Recuero and García-París, 2011). These data contrast with the apparent absence of *L. helveticus* in the northern fossil record of the Late Pleistocene, indicating that its glacial refugia were possibly located in the south.

The herpetofaunal assemblage of the archaeological site of Las Orcillas-1 in Navarre is of a later date. Concretely, the archaeological remains of levels C.II-I from Las Orcillas, which are assigned to the Microlaminar Epipaleolithic and dated to 8610 ± 50 B.P., locate the herpetofaunal assemblage in the late Pre-Boreal stage (Fernández et al., 2010). The association is formed by *B. spinosus*, *B. calamita*, *T. lepidus*, *M. monspessulanus*, *Natrix* sp. and *Zamenis-Rhinechis* (= *Elaphe* sp. sensu lato) (Fernández et al., 2010). This assemblage includes two thermophilic Mediterranean species, the lizard *T. lepidus* and the snake *M. monspessulanus*, this being the oldest Holocene record for *T. lepidus* in the northern Iberian Peninsula. It also includes the possible presence of other species typical of warm environments, such as *Z. scalaris*.

At the western end of the northern Iberian region, in Galicia, the Upper Unit of Valdavara-1 also presents a more recent assemblage with the presence of thermophilic Mediterranean species. The Upper Unit is ascribed to the Chalcolithic and is dated to 4490 ± 40 B.P. (Vaquero et al., 2009). The assemblage from this level is formed by *C. lusitanica*, *Discoglossus* cf. *galganoi*, *B. spinosus*, *R. iberica*, *C. striatus*, *A. fragilis*, *T. lepidus*, *N. maura*, *Coronella* cf. *austriaca*, *M. monspessulanus* and *Vipera* sp. (Blain et al., 2009b; López-García et al., 2011b). The frog *R. iberica*, an Iberian endemism that is ecologically very similar to *R. temporaria*, has its oldest record in level 1 of Cueva Millán, dated to MIS 3 (Esteban and Sanchiz, 1990; Díez et al., 2008), and reappears during MIS 1 in the Upper Unit of Valdavara-1. *M. monspessulanus* and *T. lepidus* appear again in association in the Upper Unit of Valdavara-1, also accompanied by another thermophilic species that makes its first postglacial appearance in the northern region, the frog *D. galganoi* (López-García et al., 2011b). *C. lusitanica* also appears for the first time in this region; this is a salamander whose distribution is currently limited to northwestern Iberia (Blain et al., 2009b). Another species typical of this region has been identified in the Upper Unit of Valdavara-1, the skink *C. striatus* (López-García et al., 2011b), which is also present in levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014). The genus *Lacerta*, which has no fossil record with specific-level ascription in the Atlantic-Cantabrian region, includes another reptile typical of northwestern Iberia, *L. schreiberi*, as well as *L. bilineata* for the northern area. Large-sized lizards assigned to *Lacerta* sp. have been identified in the Lower Unit of Valdavara-1 (López-García et al., 2011b) and level 1 of Cobrante (Martín et al., 2009).

The prehistoric assemblages from Orcillas-1 and Valdavara-1 possibly indicate the existence of two colonization routes towards the north of the Iberian Peninsula for species of Mediterranean influence and for hygrophilous species less tolerant to cold climates and glacial conditions. The eastern route, represented by Orcillas-1, would consist of the Ebro Valley and, according to the fossil record, would have been used by a Mediterranean herpetofauna (e.g., *T. lepidus*, *M. monspessulanus* and possibly *Z. scalaris*). The western route, marked by Valdavara-1, would be located on the Atlantic coastline running towards the Galician coasts and would have been used by species of Mediterranean origin (e.g., *D. galganoi*, *T. lepidus* and *M. monspessulanus*) as well as typically western species (e.g., *C. lusitanica* and *L. schreiberi*), and generalist species and/or species tolerant to Euro-Siberian conditions (e.g., *N. maura* and *C. striatus*), to colonize northwestern Iberia and the Cantabrian fringe.

Given our imperfect knowledge of the fossil record, molecular genetics is a discipline that can clarify expansive movements during postglacial colonization. Molecular studies of current populations of *C. lusitanica* are consistent with the proposed scenario, with two clades separated by the River Mondego, it being the northern population that underwent a postglacial expansion towards Galicia and Asturias (Alexandrino et al., 2000, 2002, 2005, 2007). The data provided by mitochondrial DNA show the existence of four clades of *L. schreiberi*. The northwestern clade has less genetic diversity and a greater geographical distribution, related to a very rapid recent expansion (Paulo et al., 2001), an expansive colonization process also documented in its nuclear DNA (Godinho et al., 2008). In the northwestern region, a chronologically recent expansive pattern has also been documented in *P. bocagei* (Pinho et al., 2007a). By contrast, *C. striatus* shows two distinct clades, the first distributed in the south of the Iberian Peninsula and the second spanning northern Iberia, the south of France and northwestern Italy. This second clade has a uniform genetic composition with a low level of diversification, which corresponds to a rapid and recent expansion, possibly postglacial (Carranza et al., 2008). *C. girondica* also shows a similar phylogeographic pattern, with three clades in European territory: two clades are limited to the Baetic region and southwestern Iberia, in contrast to the third clade, characterized by low genetic diversity, which covers the rest of the Iberian Peninsula, southern France, and northern and central Italy, and is the result of a recent expansion (Santos et al., 2012). *N. maura* has two well-differentiated clades in the Iberian Peninsula, a southern one based in the extreme south of Andalusia and another clade found in the rest of the Iberian Peninsula, which would have also colonized central and southern France, western Switzerland and northwestern Italy in the course of the Holocene (Joger et al., 2006).

Z. longissimus is another snake that makes its first appearance in the northern area during the Holocene. This also represents its first appearance in the Iberian prehistoric record. Accordingly, its first record corresponds to levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014), followed by the Aizkoltzo sequence (Murelaga et al., 2008) and the Chalcolithic level of El Mirón (Sanchiz et al., 2012). Phylogenetic analyses have suggested the expansion northwards of *Z. longissimus* during the Holocene

Climate Optimum (*ca.* 8000-5000 B.P.) from two glacial *refugia* separated by the Alps, reaching its maximum latitudinal range in the Danish Peninsula. After this warm climate phase its distribution recoiled southwards, leaving isolated present-day populations in Germany and the Czech Republic (Musilová et al., 2010). In the Iberian Peninsula it has colonized regions of the Pyrenees, in addition to which it has two separate populations, one in the Picos de Europa (Cantabria) and another in the Galician Massif which would be the result of a postglacial colonization and the subsequent retraction of its Iberian distribution (Ayllón et al., 2010; Cabana et al., 2014). The chronology of the Iberian sites with a record of *Z. longissimus*, coupled with the existence of these isolated populations, is consistent with the pattern proposed on the basis of phylogenetic studies (Musilová et al., 2010), although one might advance to the early Holocene the southern expansion of this snake. *H. viridiflavus*, another snake originating from the Italian Peninsula, which appears in levels N.II and N.I of Santa Catalina (Bailon and García-Ibaibarriaga, 2014), presents a similar phylogeography, although there are no molecular data for the Iberian populations. The closest studied populations are from France; these are the result of a recent colonization from the western Italian clade of *H. viridiflavus* (Nagy et al., 2002).

In contrast, data provided by the genetic studies of other Iberian species make caution essential when drawing conclusions based only on the fossil record as currently known. *Z. vivipara* is a Euro-Siberian lizard with a wide Palearctic distribution (Dely and Böhme, 1984), although in Iberia it is currently restricted to the Cantabrian fringe and the Pyrenees (Braña and Bea, 2002). This distribution pattern, along with its apparent absence from the Iberian fossil record, may suggest a postglacial colonization from Central Europe, where it has a fossil record during the Pleistocene (Holman, 1998). Nevertheless, phylogeographic genetic studies present a diversified situation, with five clades present in its Iberian distribution area, which were generated by vicariant processes throughout the Pleistocene (Milá et al., 2013). Similar phylogeographies are repeated in the case of two lizard taxa with an Iberian distribution, *P. muralis* (Salvi et al., 2013) and the genus *Iberolacerta* (Crochet et al., 2004). This leads us to propose a long evolutionary history within their own territory; apparent absences in the known fossil record are explained by the difficulty of their taxonomic identification from osteological characters (Barahona, 1996; Barahona and Barbadillo, 1997), making greater efforts necessary in this field. These taxa may be behind the indeterminate lizards of levels 9–7, 5 and 2 of Askondo (Garcia-Ibaibarriaga et al., 2015), levels P11-3 and P1 of El Portalón (López-García et al., 2010b), and cf. *Podarcis* of levels D, C and B of Antoliñako Koba (Zubeldia et al., 2007).

During MIS 1 significant changes are detected in the composition of the assemblages of reptiles and amphibians, though most of them are still dominated by the same species present in the sequences of MIS 3 and MIS 2: *A. obstetricans*, *A. fragilis*, *B. calamita*, *B. spinosus*, *R. temporaria* (or *R. temporaria-iberica*) and the genus *Vipera*. For example, the assemblages of levels IV, III and II of Erralla (Esteban and Sanchiz, 1985), levels *Balm*, *Almp*, *Slnc*, *Arcp*, *Slm* and *Lsm* of Santimamiñe (Murelaga et al., 2011), level 2 of Cobrante (Martín et al., 2009), levels 3 and 2 of Askondo (Garcia-Ibaibarriaga et al., 2015), level A of Antoliñako Koba (Garcia-Ibaibarriaga et al., 2015) and the Bell Beaker level of the dolmen of Errekatxuetako Atxa (Murelaga et al., 2007) are exclusively composed of taxa from the previously mentioned herpetofaunal association.

The midwife toad *A. obstetricans*, with representation through MIS 2 in the sequences from Portalón de Atapuerca (López-García et al., 2010b) and Erralla (Esteban and Sanchiz, 1985), disappears from the fossil record of the Pleistocene part of MIS 1. It then reappears in level N.1 of Cobrante, which is ascribed to the Holocene (Martín et al., 2009). Subsequently, it also appears in the Neolithic and Bronze Age levels of El Mirón (Sanchiz et al., 2012) and in the dolmen of Errekatxuetako Atxa (Murelaga et al., 2007). On an ecological level, this absence, if it genuinely occurred and is not the product of a possible taphonomic bias, could simply be correlated with the absence of permanent water points between Heinrich Event 1 and the Pre-Boreal Holocene stage. Such points are necessary for it to complete its larval stage (Bosch, 2014).

Nonetheless, this is contradicted by the presence of species closely linked to an aquatic environment such as *S. salamandra*, cf. *I. alpestris* and cf. *L. helveticus* in the latest Pleistocene sequence from Santa Catalina and Laminak II (Sanchiz and Esteban, 1994; Bailon and García-Ibaibarriaga, 2014) and the indeterminate salamander from level B of Antoliñako Koba (Zubeldia et al., 2007). The toad *B. calamita* had a greater distribution in the paleontological record than at present. Today its distribution in the Cantabrian area is very scarce and is limited to the southernmost fringe and two coastal populations in the Basque Country (Tejedo and Reques, 1997; Reques and Tejedo, 2002; Garin-Barrio et al., 2007). In the Late Quaternary record, it appears in a total of 20 assemblages: the entire sequence from Portalón de Atapuerca and Santa Catalina (López-García et al., 2010b; Bailon and García-Ibaibarriaga, 2014), levels V and IV of Erralla (Esteban and Sanchiz, 1985), levels Camr-Csn and Lsm of Santimamiñe (Murelaga et al., 2011), level Ll.15–12 of Aizkoltzo (Murelaga et al., 2008), levels C.II-I of Las Orcillas-1 (Fernández et al., 2010) and possibly levels 4 and 3 of Cobrante (Martín et al., 2009). Today *B. calamita* is absent in the vicinity of Cobrante, Aizkoltzo, Erralla, Santimamiñe and Santa Catalina, but present in the territories of Las Orcillas-1 and Portalón de Atapuerca. It is also present in the area around Valdavara-1 and Peña Larga (AHE, 2016), although it does not appear in the archaeological record of these sites.

4.2. Northeastern region

The dominant species in the latest Quaternary in the northeastern fossil record, which basically includes Catalonia and Aragon, are *A. obstetricans*, *B. calamita*, *R. temporaria*, *A. fragilis* and to a lesser extent *B. spinosus*, *C. girondica* and *P. punctatus*. This is an assemblage with hygrophilous tendencies, although the association of *B. calamita* and *P. punctatus* indicates the existence of irregularities in the water regime that may be associated with a Mediterranean influence.

R. temporaria is a Euro-Siberian frog that in the Iberian Peninsula is restricted to the area formed by the axis of the Cantabrian Mountains and the Pyrenees and within the Mediterranean region is only present in the Montseny Massif, due to the latter's Pyrenean influences (Esteban and García-París, 2002). In these regions it lives in wetlands, from mountain meadows to deciduous forests of *Quercus* and *Fagus* (Álvarez, 2014). It does not tolerate ambient temperatures over 26 °C and needs average temperatures below 5 °C in autumn and winter to carry out its reproductive cycle (Balcells, 1975). *A. obstetricans* is another anuran especially associated with high rainfall areas. Away from these, its distribution is restricted to mountainous systems or areas that allow permanent water points, because of its particularly long larval development lasting from 91 days to three years (Bosch, 2014). *C. girondica* is a snake with an extensive western Mediterranean distribution and presents great altitudinal and environmental variation, although its main ecological requirement is the presence of small lizards (genera *Psammodromus* and *Podarcis*), its main prey (Santos and Pleguezuelos, 2009). The herpetofaunal taxa present in MIS 3 are mainly generalists and species tolerant to Mediterranean conditions as well as to Euro-Siberian climates. Noteworthy is the practical absence of thermophilic taxa by contrast with the recurrent

appearance of *R. temporaria*, despite it being an area in direct contact with the Mediterranean Sea. In fact, *R. temporaria* appears outside its current distribution in the latest Pleistocene sequences of Teixoneres, Abric Romaní and Galls Carboners; this latter site is located 120 km from the current southern boundary of the *R. temporaria* distribution on the Montseny Massif. Further, the Pleistocene citations of *V. aspis* from Teixoneres and Abric Romaní lie outside its current distribution range.

Very common species in the Mediterranean area that have significant fossil records in contemporary sites in southern Iberian areas, such as the lizard *T. lepidus* or the snake *N. maura*, only appear in the northeastern region in the Holocene levels of Balsa la Tamariz (Laplana and Cuenca-Bescós, 1995) and Cova Colomera, respectively (López-García et al., 2010a). The thermophilic Mediterranean gecko *T. mauritanica* also has its only record in this latter cave, in its most recent phase (level A.sup., 3490 ± 50 B.P.) (López-García et al., 2010a). The snake *M. monspessulanus*, closely linked to the Mediterranean bioclimate, has its only record in the latest Pleistocene in level IIb of Cova Teixoneres, assigned to MIS 3 (ca. 35,000 B.P.) (López-García et al., 2012b, 2014a; Talamo et al., 2016). This snake reappears in the northeastern record until the Bronze Age level of Balsa la Tamariz (3600–3400 B.P.), where appear in concurrence with *T. lepidus* (Laplana and Cuenca-Bescós, 1995). The thermophilic assemblage from Balsa la Tamariz (*P. cultripes*, *T. lepidus* and *M. monspessulanus*) in the Ebro Valley, combined with the presence of *T. mauritanica* in the last phase from Cova Colomera, located on one of the tributaries of the River Ebro (López-García et al., 2010a), may possibly be correlated with the existence of a natural corridor along the Ebro Valley and its tributaries, from which species native to the Mediterranean area would have colonized the Iberian inland during the Holocene climatic progression.

For the newt *T. marmoratus*, absent in the regional fossil record, different routes of colonization have been proposed for its two eastern populations: the one located in the province of Girona would be the result of a postglacial colonization from Roussillon on the other side of the Pyrenees, while the populations of southern Catalonia and central Aragon would have come from the Navarra-Rioja area; this species possibly used the River Ebro to colonize as far as its final section (Llorente et al., 1995; Montori, 2014). The River Ebro would have thus served as a route running in both directions, for Mediterranean species leading inland towards the north of the Iberian Peninsula and for hygrophilous species from the north leading to the new environments that had opened up on the eastern periphery.

The snake *C. austriaca*, with a record in MIS 3 in levels IIb and II from Cova Teixoneres (López-García et al., 2012b, 2014a) and from Canyars (Daura et al., 2013; López-García et al., 2013, 2014a), is the only species present in the northeastern prehistoric record that does not appear in the current assemblages. Another species of the genus *Coronella*, *C. girondica*, which appears on levels 8 to 5 of Cova Xaragalls (López-García et al., 2012c) and C15, C14–13 and C12 of Cova Colomera (López-García et al., 2010a), is currently distributed in a greater number of assemblages and has a greater distribution range. *C. austriaca* is much less thermophilic than *C. girondica* and the altitudinal and environmental segregation of these two species has been confirmed in the Iberian Peninsula when they are in sympatry (Galán, 1988; Lizana et al., 1988; Morales et al., 2002). The absence of *C. austriaca* in areas where it was present in the past and the currently greater distribution of *C. girondica* can be correlated with altitudinal changes in the bioclimatic levels, as proposed for the sequence from MIS 5c to MIS 4 of Cueva del Camino (semi-arid climate during warm periods to a wet mid-latitude climate during cold periods) (Blain et al., 2014b).

The absence of sites dating from MIS 2 and the poor data from MIS 1 for this area of Iberia preclude a deeper evolutionary comparison of its herpetofauna. However, the ongoing studies of the microvertebrate remains from Cova Bonica, Balma del Gai, l'Arbreda and Coves del Toll will increase what is known of the composition of the herpetofauna record and its main biogeographic changes in the Catalan area during the Late Quaternary. The current herpetofaunal composition of the northeastern region suggests a postglacial recolonization of this territory by thermophilic species along the Mediterranean coast from the Valencian Country and inland through river valleys, especially the Ebro and its tributaries. In parallel, other species would have entered from the north by the Mediterranean coast and the eastern edge of the Pyrenees, originating from the south of France and the west of Italy, as seen for the Cantabrian region with *Z. longissimus*, *H. viridiflavus* and *L. bilineata*. Finally, native Pyrenean species might have used the same river valleys to penetrate into the Pre-Pyrenean foothills and the Catalan central basins that were favorable for colonization. This would have been in addition to the existence in these mountainous areas of interglacial *refugia* for species from Euro-Siberian and/or Alpine environments, as proposed for Cova Colomera and the Serra del Montsec for species such as *R. temporaria* and *A. fragilis* (López-García et al., 2010a).

4.3. Central and southern regions

B. calamita, *T. lepidus*, *B. spinosus*, *Z. scalaris* and, to a lesser extent, *P. cultripes*, *T. hermanni*, *M. monspessulanus*, *P. waltl* and *V. latastei* are the best-represented species in the paleo-archaeological sites of the central and southern Iberian Peninsula from MIS 3 to MIS 1. Together they constitute an association of herpetofauna typical of the majority of the thermophilic environments in current Mediterranean Iberia (with the exception of *T. hermanni*, extinguished regionally). As mentioned above, they form an assemblage with a predilection for dry Mediterranean environments with a markedly seasonal water regime and the presence in the landscape of both open areas and scrubland and forests.

The large lizard *T. lepidus* is one of the most characteristic species of the Mediterranean bioclimate in southwestern Europe, to the extent that the northern boundary of its distribution coincides with the boundary between Mediterranean and Euro-Siberian bioclimates (Cheylan and Grillet, 2005). *B. spinosus* is a very generalist toad that occupies practically all habitats characteristic of the Iberian Peninsula, from the thermo-Mediterranean pre-montane areas to the Euro-Siberian mountains (Ortiz-Santaliestra, 2014), while *B. calamita*, also generalist and fairly widespread, prefers open areas with sparse vegetation or low cover and high insolation, associated with a higher degree of environmental aridity and higher annual average temperatures (Gómez-Mestre, 2014). The viper *V. latastei* is a species typical of humid, sub-humid and semi-arid Mediterranean climates with a preference for plains and warm areas, rocky areas with scattered vegetation cover, as well as forest glades (Brito, 2011). *P. waltl* is a fully thermophilic newt, and is currently the only salamander present in the eastern Iberian Mediterranean area, where it occupies the thermo-Mediterranean, meso-Mediterranean and supra-Mediterranean bioclimates (Montori et al., 1997, 2002).

Also characteristic of the fossil record of this region is the presence of *T. hermanni*, which during the Late Pleistocene presents a continuous record from the previous interglacial (MIS 5e) until the period before the Last Glacial Maximum (MIS 2), confirming the prehistoric distribution of this land tortoise in the Iberian inland and along the Atlantic coast. These are regions where it is now extinct (Morales and Sanchis, 2009) and *T. hermanni* is currently associated with limited coastal areas with a Mediterranean climate in the northern half of the Iberian Mediterranean coast, although in

the east of its Mediterranean distribution in Italy and the Balkans it also appears in sub-Mediterranean climates, living in open environments, such as glades in wooded areas, shrublands or dune grasslands (Bertolero, 2010). Temperatures mark the viability of *T. hermanni* embryos, which die at temperatures below 25 °C or above 35 °C (Eendebak, 1995), possibly serving to establish one of its climatic barriers, based on the maximum/minimum temperatures of the months between the egg laying and eclosion from mid-May to early October (Bertolero, 2010).

The association of species typical of the Atlantic Iberian area such as *T. pygmaeus*, *C. striatus* or the genus *Lissotriton* in the Pleistocene levels of Gorham's Cave (MIS 3–1, 32,500–10,800 B.P.), along with predominantly thermo-Mediterranean faunal and botanical records, suggest the existence of a southern glacial *refugium* for the herpetofaunal species of the western Iberian Peninsula during the most critical climatic phases of the Late Pleistocene, within their parameters of habitability but outside their current distribution areas (Blain et al., 2013). A clear example of this approach is the current absence of the genus *Lissotriton* in the Iberian part of the Strait of Gibraltar, the *L. boscai* populations of the Doñana National Park being the closest to Gorham's Cave, which is located more than 120 km away (Díaz-Paniagua, 2002). This raises the possibility that there was first an expansion of its distribution towards the south during the last glacial phase and subsequently a retraction of the populations towards the north during the Holocene.

The continued presence of the gecko *T. mauritanica* is significant from the previous interglacial (MIS 5), with the sequence from Vanguard's Cave (Gleed-Owen, 2001; Gleed-Owen and Price, 2012), to the present, with records ranging from MIS 3 to MIS 1 in the sequences from Boquete de Zafarraya and Gorham's Cave (Barroso and Bailon, 2003; Barroso et al., 2003; Blain et al., 2013). This fossil record confirms its indigenous Iberian character from prior to the Holocene and contradicts the theory of its introduction by humans in recent times (Mayol, 1985; Harris et al., 2004a). This also coincides with the genetic diversity of the *T. mauritanica* populations observed in central and southeast Iberia, with three different lineages identified (Harris et al., 2004b; Perera and Harris, 2008), the central populations presenting an old mitochondrial lineage that refutes the theory of its recent introduction and corroborates its autochthony, at least in the case of these central populations. In fact, the genetic distance among the Iberian populations of *T. mauritanica* is so high that it could possibly be ascribed to two different species, the native central species and a recently introduced species on the southern and eastern littoral (Rato et al., 2016). As yet, there is no description of osteological characters that would make it possible to differentiate between these two new species. The absence of *H. turcicus*, the other gecko currently present in the Iberian Peninsula, in the fossil record of the Late Pleistocene and the genetic homogeneity of its European populations, including the Iberian populations, raise the possibility of a very rapid dispersion from a point of origin in the eastern Mediterranean Sea in recent times and possibly caused by humans (Carranza and Arnold, 2006; Mateo et al., 2011). Later, it would have colonized the Iberian Peninsula from a bridgehead in North Africa, although the mitochondrial homogeneity of the European clade (clade A) may be due to selective sweep processes and not just a recent expansion (Rato et al., 2011). However, it should be noted that *H. turcicus* is a small gecko with a fragile osteology that may suffers problems of preservation in the fossil record.

The herpetofaunal assemblage of level A of Sala de las Chimeneas from Cueva de Maltravieso in Extremadura, dated to the final phase of the Last Glacial Maximum (between 19,500–18,700 cal. B.P. and 19,700–18,750 cal. B.P.) (Bañuls-Cardona et al., 2012), is composed of *B. spinosus*, *B. calamita*, *P. perezi*, *T. lepidus*, (cf.) *N. maura*, *C. girondica* and *V. latastei*, an association that shows the survival of a thermophilic Mediterranean herpetofauna within the Iberian Peninsula even in the most critical glacial times of the latest Pleistocene. The herpetofaunal fossil record of central and southern areas is rich if compared with the other two regions analyzed, even though the central area is lower in the number of species than the Andalusian and Portuguese regions. This is the case with the MIS 1 sequence from Peña de Estebanvela prior to the Younger Dryas, with the concurrence of the anurans *Alytes* sp. and *B. calamita* in level VI (14,450 ± 80 B.P. & 14,200 ± 50 B.P.) or only *B. calamita* in levels IV, III and II during the Younger Dryas (12,530 ± 60 B.P. to 11,400 ± 120 B.P.) (Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013). However, in level I of Estebanvela de Peña, dated at between 11,330 ± 50 cal. B.P. and 10,640 ± 60 cal. B.P., there appears the association of *B. calamita*, *T. lepidus*, *M. monspessulanus*, *Z. scalaris*, (cf.) *Coronella* sp. and *V. latastei*, similar to that documented in level A of Sala de las Chimeneas. In this case it is an assemblage of a markedly Mediterranean herpetofauna occurring at a level assigned to the cold climatic phase of the Younger Dryas. Both cases, level A of Sala de las Chimeneas and level I of Peña de Estebanvela, seem to indicate a climate scenario that is less aggressive than might have at first been thought for the thermophilic and/or typical Mediterranean species of the Iberian inland during the latest Pleistocene. Another thermophilic assemblage dating to MIS 2 is that documented in level IV of Cueva Higueral de Valleja (18,300 ± 4800 B.P. and 15,500 ± 3700 B.P.), in the region of Cadiz, where appear in concurrence *B. calamita*, *T. mauritanica*, *N. maura*, *M. monspessulanus*, and *Z. scalaris* (Jennings et al., 2009).

In the eastern Mediterranean strip of the studied area, the herpetofaunal fossil record of the Valencian Country is characterized by the scarcity of publications of prehistoric assemblages and the high degree of mono-specific citations in the literature, which is basically monopolized during the Late Pleistocene by *T. hermanni* and *Testudo* sp. (Morales and Sanchis, 2009; Sanchis et al., 2015), a species easily identifiable in the zooarchaeological record by contrast with the non-chelonian herpetofauna. Thus, in the Late Pleistocene of the Valencian Country, this typically Mediterranean turtle is documented in the MIS 5e levels of Cova de Bolomor (Fernández Peris, 2007; Blasco, 2008), the Mousterian levels of Cova Negra of Xàtiva (Pérez Ripoll, 1977), in Abrigo de la Quebrada (Sanchis et al., 2013), Abric del Salt (Morales and Sanchis, 2009; Pérez Luís, 2014), Abric del Pastor (Galván et al., 2008; Sanchis et al., 2015), San Luís of Buñol (Fernandez Peris and Martínez Valle, 1989) and the Pleistocene sequence of Cova Canet of Aielo de Malferit (Morales and Sanchis, 2009). Further, the presence of indeterminate chelonians is recorded in the Cova de Dalt Tossal de la Font of Vilafamés, possibly associated with an accumulation caused by a group of hyenas (Saladié et al., 2010). In addition to *T. hermanni*, the presence of the toad *B. spinosus* (Luis Perez, 2014) has also been identified in level X of Abric del Salt. In the Valencian Pleistocene record, there is evidence of the human consumption (by *H. neanderthalensis*) of turtles in Bolomor, Abrigo de la Quebrada and Abric del Pastor (Blasco, 2008; Galván et al., 2008; Sanchis et al., 2013, 2015).

As regards the Valencian Holocene, citations of the presence of *Testudo* sp. from the Chalcolithic archaeological site of Ereta del Pedregal (Pérez Ripoll, 1990) have recently been assigned to *M. leprosa* and Emydidae/Geoemydidae indet. (Morales and Sanchis, 2009). An individual belonging to *M. leprosa* has also been identified in the Neolithic levels of Cova de l'Or (Pérez Ripoll, pers. com.). In Lloma de Betxí, dated to between 2100 cal. B.C.E. and 1600 cal. B.C.E. and assigned to the Valencian Bronze Culture (De Pedro, 2004), *B. spinosus*, *M. leprosa*, *T. lepidus* and *Elaphe* sp. have been identified in concurrence (Tormo and De Pedro, 2013); this latter taxon may be *Z. scalaris*, the only species from the complex of

the genus *Elaphe* sensu lato that is present in the Valencian Country, which also includes *Z. longissimus* (Pleguezuelos, 2009; Rubio and Gosá, 2010). *M. leprosa* is also documented in phase III of the Bronze Age from Pic dels Corbs, dated to between 1400/1350 cal. B.C.E. and 1100/1050 cal. B.C.E. (Barrachina and Sanchis, 2008).

The prehistoric herpetofauna known from the final Late Pleistocene and the Late Holocene of the Valencian Country is quite poor when compared with the rest of the Iberian Peninsula, both in the number of sites with a published record and in the number of taxa identified, by contrast with the relatively good knowledge of its archaeological record. Assemblages such as those from Lloma de Betxí with *B. spinosus*, *M. leprosa*, *T. lepidus* and *Elaphe* sp. (= *Z. scalaris*?) and the combination of *T. hermanni* and *B. spinosus* from Abric del Salt represent exceptions within the Valencian herpetofaunal fossil record.

The Portuguese Atlantic region also suffers from a scarcity of sites with a published prehistoric herpetofauna for the period studied. However, by contrast with the Valencia Country, two Portuguese sites have assemblages with a significant number of species: Gruta da Figueira Brava (MIS 3) and Guia de Albufeira (Pleistocene phase of MIS 1) (Crespo et al., 2000; Crespo, 2002). In both herpetofaunal associations there are typically thermophilic species such as *B. cinereus-mariae*, *T. lepidus* and *P. cultripes*, along with other species such as *P. waltl* and *A. erythrurus*, which also have a fossil record in the Andalusian Late Pleistocene. In addition, there are chelonian citations from Gruta Nova da Columbeira (*T. hermanni* and Emydidae indet., MIS 3), Gruta do Caldeirão (*T. hermanni* and *M. leprosa*, MIS 2) and Gruta do Escoural (*T. hermanni*, MIS 2), as well as the turtle assemblage from Gruta da Figueira Brava (*T. hermanni* and *E. orbicularis*, MIS 3) (Crespo et al., 2000; Crespo, 2002; Morales and Sanchis, 2009; Nabais, 2012).

Apart from its appearance in Gruta do Caldeirão, *M. leprosa* does not have a known record for MIS 3 and 2 in the Iberian Peninsula. However, the number of citations of this turtle increases greatly during the Holocene, above all from the Neolithic onwards (Jiménez Fuentes, 1986; Budó et al., 2005; Félix et al., 2006; Barrachina and Sanchis, 2008; Morales and Sanchis, 2009; Tormo and De Pedro, 2013). In contrast, the other freshwater Iberian turtle, *E. orbicularis*, has a greater number of Late Pleistocene records, namely in the Mousterian sequences from Figueira Brava and Gruta Nova da Columbeira (Emydidae indet.), level IV of Gorham's Cave (Emydidae indet.) and level NM14 of Cueva de Nerja (Jiménez Fuentes, 1986; Gómez and Jiménez Fuentes, 1998; Crespo, 2002; Blain et al., 2013). Genetic studies of current Maghrebian and Iberian populations of *M. leprosa* suggest that it recently colonized the Iberian Peninsula from populations to the north of the Atlas Mountains or even from a bridgehead at the southern tip of the Iberian Peninsula itself, because the Strait of Gibraltar was possibly not an impermeable barrier to genetic exchange between *trans*-Mediterranean populations of freshwater turtles (Fritz et al., 2006; Velo-Antón and Pinya, 2015a). The genetic scenario amongst the Iberian populations of *E. orbicularis* is much more diverse, with four different clades identified, at least one of them endemic. Of the remaining three, one appears on both sides of the Strait of Gibraltar and the other two clades have eastern and *trans*-Pyrenean origins and appear in the northern half of the Iberian Mediterranean coast and the Ebro Valley (Velo-Antón et al., 2015; Velo-Antón and Pinya, 2015b). Therefore, the data provided by genetic studies are consistent with the scenario presented by the fossil record, with the possible extinction of *M. leprosa* from most (or even all) of the Iberian Peninsula, while *E. orbicularis* maintained populations in Iberia during the Late Quaternary, being a much less thermophilic species than *M. leprosa*. The onset of the current interglacial would have allowed *M. leprosa* to recolonize the Iberian Peninsula from the Straits of Gibraltar, as well as permitting the arrival of new populations of *E. orbicularis* from the Maghreb and *trans*-Pyrenean Europe.

As regards species with no fossil record between MIS 3 and MIS 1, there are citations of *Alytes* sp. and *Lissotriton* sp. from Gorham's Cave (Blain et al., 2013) and of *Alytes* sp. from Peña de Estebanvela (Sanchiz and Barbadillo, 2007; Sanchiz and Bailon, 2013), which by their geographical distribution could correspond to *A. cisternasii*/*dickhilleni* and *L. boscai* and to *A. obstetricans*/*cisternasii*, respectively. *H. meridionalis* could have its last Pleistocene fossil record in the Mousterian levels from Vanguard's Cave of Gibraltar, dated to MIS 5 (Gleed-Owen, 2001; Gleed-Owen and Price, 2012), therefore being absent from the rest of the Pleistocene and from the sites hitherto known for the Holocene, when it could have crossed the Strait of Gibraltar to colonize southwest Iberia (Tejedo and Reques, 2002).

Finally, another species of North African origin, *C. chamaeleon*, has a single zooarchaeological record in the Bronze Age levels of Cueva de la Victoria of Málaga (Talavera and Sanchiz, 1983), being absent throughout the rest of the fossil record of the Iberian Quaternary. This has not been included in the regional data matrix because it is a mono-specific citation. The statistical methods applied to the regional data matrix suggest a scenario of great stability in the herpetofaunal composition of the center and south of the Iberian Peninsula, with little observable change by chronological level. Climatic and environmental changes linked both to the last glacial phase and the subsequent interglacial onset seem not to have had large impacts on the herpetofaunal composition of this area. The detected biogeographic changes are the contraction of the southern boundary in the distribution of some taxa (e.g., genus *Alytes* and L. *boscai* in the Gibraltar region), the possible recolonization by *M. leprosa* from the Maghreb, and the entry of new species such as *H. meridionalis* and *C. chamaeleon*, also from North Africa. In the future, data on the prehistoric herpetofauna of central and southern Iberia are expected to increase from the ongoing study of significant sites such as Pinilla del Valle and new campaigns in the caves of Gibraltar, Castillejo del Bonete and Maltravieso.

4.4. General discussion

The apparent absence of some species in the fossil record, especially those of smaller size, may be due to multiple factors of destruction and selection, processes also observed in the bias towards specific skeletal elements (Esteban and Sanchiz, 1985). At an ecological level, the lack of specialized predators of particular species of amphibians and reptiles reduces the taphonomic bias generated by them to criteria such as the size of prey or individual visibility at hunting time (Blain, 2009), which may generally affect species of smaller sizes.

One of the most difficult groups when it comes to species-level taxonomic identification is Lacertidae, especially the species of small size, which includes the genera *Podarcis* and *Psammodromus*. *Podarcis* is a lizard genus that currently shows a large specific diversity, manifest in its phylogenetic complexity in the Iberian Peninsula (Kaliontzopoulou et al., 2011). Within this genus, *P. hispanica* (sensu lato) is a paraphyletic taxon that groups most of the rupicolous Iberian lizards, with a distribution that covers most of the Iberian Peninsula up to the isotherm of 14 °C and with significant insolation requirements (Sá-Sousa and Pérez-Mellado, 2002). With the advance of molecular investigations into this taxon, at least six news species have been separated and described, *Podarcis carbonelli*, *P. bocagei*, *P. vaucheri*, *P. liolepis*, *P. guadarramae* and *P. virescens* (Harris and Sá-Sousa, 2001, 2002; Harris et al., 2002; Pinho et al., 2003, 2006, 2007b, 2008, 2009; Renoult et al., 2010; Geniez et al., 2014). Thus, *P. hispanica* sensu stricto is restricted to the Mediterranean eastern area and southeastern

Iberia (Geniez et al., 2007). Genetic analyses show that this varied and extensive speciation was the result of a rapid process of allopatric diversification that occurred in a short time period, with different lineages that appeared in relatively small geographical areas. This scenario is associated with the existence of "*refugia within glacial refugia*" in the Iberian Peninsula (Pinho et al., 2007a), a vicarious regionalization of the Iberian distribution of these species in accordance with the different climatic conditions and geographical barriers.

With a currently poor fossil record that precludes an archaeopaleontological approach because of the lack of criteria for taxonomic identification based on the skeletal remains of these new, recently described species, the correlation between the current distribution of the *P. hispanica* complex, the theoretical expansions during the postglacial period and the geographical disposition of their glacial *refugia* can be used to locate those regions that kept optimal climatic conditions for these relatively thermophilic lizards through the different Pleistocene glaciations. Furthermore, a better genetic understanding of the Iberian populations of *P. muralis*, a different species of lizard that is not part of the *P. hispanica* complex, as well as the determination of better osteological characters that may lead to its taxonomic identification in the fossil record, would permit a comparative scenario between these two taxa, since *P. muralis* is a lizard that is much more resistant to Euro-Siberian conditions, which a priori would allow greater adaptability and a wider distribution during the Pleistocene cold phases.

Currently, *P. muralis* occupies the Iberian Euro-Siberian fringe, but also presents two southern relict populations limited to the Central System and the Iberian System mountain ranges that are isolated from the northern populations (Pérez-Mellado, 2002; Diego-Rasilla, 2009), suggesting a greater distribution in the past. At the moment, the data available from its Iberian populations suggest the existence of two endemic clades, clade 2 in the Cantabrian Mountains and clade 3 in the Central System and the Iberian System, plus a third clade in the Pyrenees which is also distributed in western France (clade 1). Furthermore, it has been found that the discontinuity in the distribution of its Iberian populations does not correspond to a genetic discontinuity, so the fragmentation process is due to recent dynamics (Salvi et al., 2013), which can be associated with the effects of climate change in the current interglacial. Two other lizards linked to Euro-Siberian climates and/or to Alpine environments, which show phylogeographies that suggest a long evolutionary history in the Iberian Peninsula, are *Z. vivipara* and the genus *Iberolacerta* (Crochet et al., 2004; Milá et al., 2013) although these have not been identified in the fossil record to date.

Another Iberian lizard, *L. schreiberi*, has four distinct lineages, two coastal clades located on the northern and southern Atlantic littoral, and two inland clades present in the Central System and in the populations of the southern mountain ranges, respectively. These inland clades and the southern coastal population are associated with possible glacial *refugia* for this lizard, the northern coastal lineage being the only one that presents an expansive distribution during the postglacial (Paulo et al., 2001, 2002a). By contrast, processes of genetic divergence reflecting east-west allopatry have been described for Iberian populations of *P. waltl*, *P. algirus*, *A. erythrurus* and *D. galganoi*, associated with the existence of two favorable climatic areas serving the function of a glacial *refugium* in southeastern and southwestern Iberia (Schmitt, 2007). In contexts beyond the reach of "classic" zooarchaeological studies due to the limitations of a purely osteological taxonomy, molecular studies provide an open window onto the distribution of species in the past and their paleoclimatic and paleoenvironmental implications, always bearing in mind the difficulty of reading and dating the genetic isolation of herpetofaunal populations.

The herpetofaunal fossil record of the Iberian latest Quaternary is very rich and varied in comparison with contemporaneous associations documented in Central Europe, which has associations of *S. salamandra*, *Triturus cristatus*, *Triturus vulgaris*, *Bufo bufo*, *Bombina bombina*, *Hyla arborea*, *Pelobates fuscus*, *R. dalmatina*, *R. temporaria*, *Pelophylax ridibunda*, *E. orbicularis*, *A. fragilis*, *Lacerta viridis*, *N. natrix* and *Z. longissimus* during the interglacial optimum, joined in the colder stages of the interglacial by the species *B. calamita*, *Bufotes viridis*, *Rana arvalis*, *L. agilis* and *C. austriaca*, together with *T. vulgaris*, *B. bufo*, *H. arborea*, *P. fuscus*, *R. temporaria*, *P. ridibunda*, *A. fragilis* and *N. natrix*. This herpetofaunal diversity is reduced drastically with the onset of the glacial phase, with associations of *B. viridis*, *R. temporaria*, *Z. vivipara* and *Vipera berus* reported, and finally only the frog *R. temporaria* in the glacial maximum (Böhme, 1996, 2010, 2000).

The Iberian scenario shows the continued presence of thermophilic species in the center and south of the Iberian Peninsula and their survival in the most critical moment of the last glacial phase (Fig. 5), the Last Glacial Maximum, with a typical Mediterranean assemblage of *B. spinosus*, *B. calamita*, *P. perezi*, *T. lepidus*, (cf.) *N. maura*, *C. girondica* and *V. latastei* in level A of Sala de las Chimeneas from Cueva de Maltravieso (Bañuls-Cardona et al., 2012). Another pleniglacial herpetofaunal assemblage that is richer than the Central European scenario has also been cited in northern Iberia, with the association of *A. obstetricans*, *B. spinosus*, *B. calamita*, *R. temporaria*, Lacertidae indet. and *Vipera* sp. in levels 6 to 3 of El Portalón de Atapuerca, also dating from the Last Glacial Maximum (López-García et al., 2010b).

Another possible comparison is with the rodent fossil record of the Iberian latest Quaternary, which is characterized by the appearance of most current species, such as *Chionomys nivalis* and *Iberomys cabrerae*, the extinction of *Pliomys lenki*, *Iberomys brecciensis* and *Allocricetus bursae* as well as the disappearance of the Iberian populations of *Microtus oeconomus*, *Microtus gregalis*, *Castor fiber* and *Hystrix brachyura* (Sesé and Sevilla, 1996; López-García, 2008). The emergence of new rodents such as *Mus spretus*, *Mus musculus*, *Micromys minutus*, *Rattus rattus* and *Rattus norvergicus* occurred throughout the Holocene, and these are species related to humans by commensalism (Sesé and Sevilla, 1996). By comparison, among reptiles and amphibians the scenario is more static and limited to the glacial restriction of thermophilic and/or Mediterranean taxa to central and southern Iberia, with the subsequent colonization by some of these species of the northern Iberian regions taking advantage of the postglacial climate improvement, but without the total extinction of any species identified in the latest Pleistocene record (Fig. 5). The appearance in the Holocene of species without an Iberian fossil record in the latest Pleistocene, such as the anuran *H. meridionalis*, the tortoise *Testudo graeca*, the gecko *H. turcicus* and the chameleon *C. chamaeleon*, has been linked to human introductions; all of them have clear phylogenetic relationships with populations located on the Maghrebian side of the Strait of Gibraltar (Pleguezuelos et al., 2008).

Z. longissimus is the only herpetofaunal case of a postglacial colonization from the other side of the Pyrenees currently verified both by the fossil record and by molecular studies (Musilová et al., 2010). However, this snake is unlikely to be the only taxon that used this route of colonization, as might have occurred with other reptiles with similar phylogeographies, such as *L. agilis* (Kalyabina et al., 2001) and *L. bilineata* (Brückner et al., 2001; Joger et al., 2001; Böhme et al., 2007), although there are no Iberian fossil records for these species. In the case of *H. viridiflavus*, which presents a postglacial fossil record in the Iberian Peninsula, the phylogeography of its Iberian populations is unknown (Nagy et al., 2002; Joger et al., 2007).

H. meridionalis, which is probably present in the Iberian Early

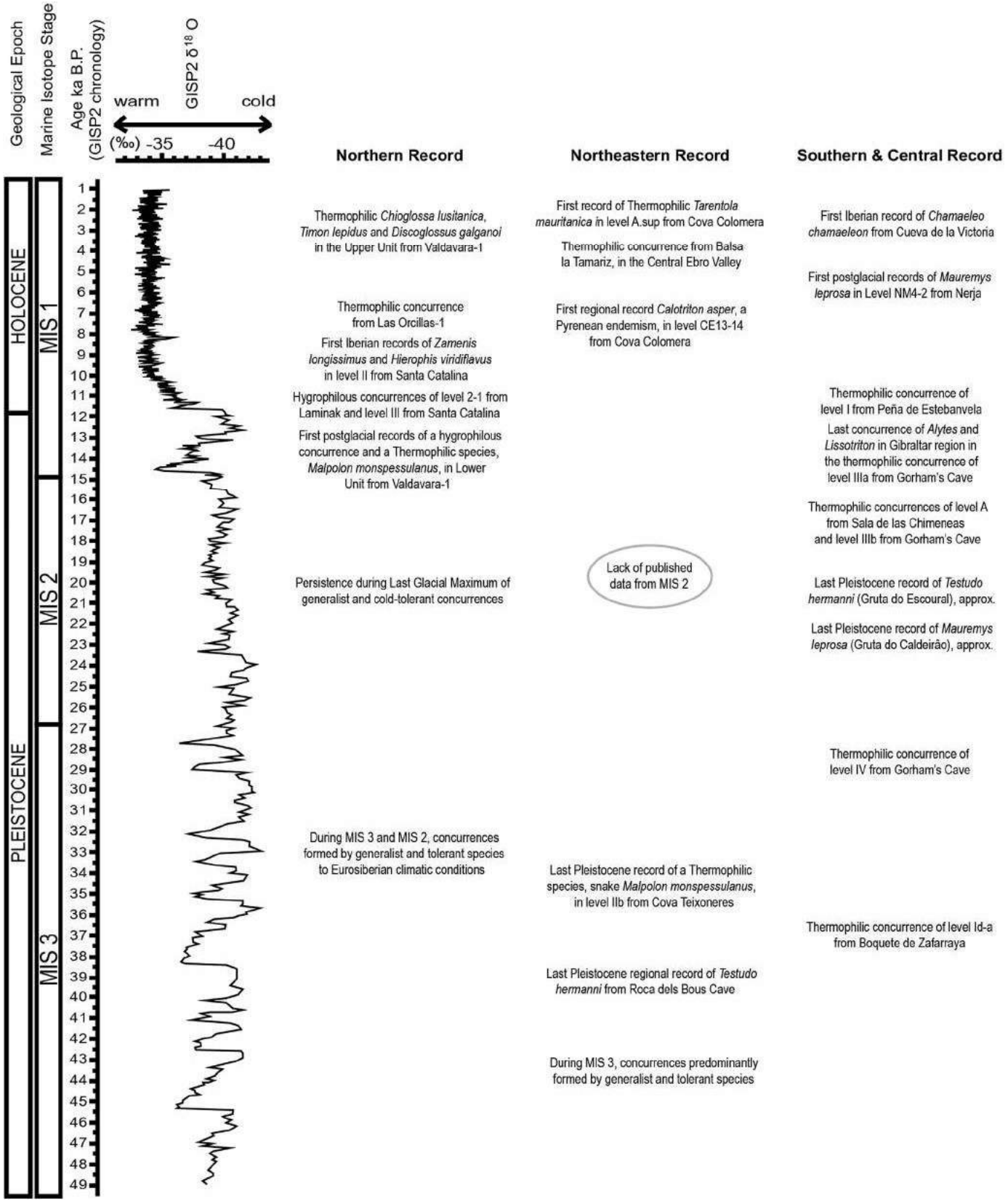

Fig. 5. Comparison of the main biogeographic changes and the most significant herpetofaunal assemblages in the Iberian Peninsula during the latest Quaternary with GISP2 oxygen isotope records (modified from Fletcher and Sánchez-Goñi, 2008).

Pleistocene (Blain, 2009; Agustí et al., 2010) but is apparently absent from the fossil record of the Late Pleistocene except for its appearance in the MIS 5b-a sequence of Vanguard's Cave (Gleed-Owen, 2001; Gleed-Owen and Price, 2011), has been reintroduced in recent times from two different areas of North Africa (Recuero et al., 2007). Something similar has been detected in the Iberian communities of *C. chamaeleon*, which were introduced from two populations in Atlantic and Mediterranean areas of the Maghreb (Paulo et al., 2002b). *H. turcicus* could have colonized the thermophilic Iberian littoral from populations in North Africa (Carranza and Arnold, 2006; Mateo et al., 2011; Rato et al., 2011). Meanwhile, the two Iberian populations of *T. graeca* share haplotypes with Maghreb populations, having reached the Iberian Peninsula either by human introduction or by natural rafting from northern Algeria in rather recent times, adding to the modern contributions of Moroccan individuals in the Doñana area (Álvarez et al., 2000; Fritz et al., 2009; Graciá et al., 2011, 2013, Graciá and Giménez, 2015). These are generally species of anthropophilic tendencies and, in the specific cases of *T. graeca* and *C. chamaeleon*, cultural linkages and magical-religious practices are known that could have led to their intentional introduction by humans (Pleguezuelos et al., 2008).

Returning to the north of the Iberian Peninsula, the reptiles *L. bilineata*, *Z. longissimus* and *H. viridiflavus* would have crossed the Pyrenees during the postglacial stage. These three species have reduced distributions in the Iberian Peninsula, basically focused on the two ends of the Pyrenees, the Basque-Cantabrian and Catalan areas (Santos et al., 2002a, 2002b; Barbadillo, 2002). In contrast to their situation in Iberia, they have an extensive and widespread distribution in Mediterranean environments of the Italian Peninsula and Sicily (Gosá and Rubio, 2013). Their restricted distribution in the Iberian Peninsula, despite their tolerance of fully Mediterranean climates and thermophilic environments, has been linked to competition with other Iberian species. *Z. scalaris* is considered the Iberian ecological equivalent of *Z. longissimus*, the two species excluding each other and appearing in sympatry only at the southern limit of the Pyrenean distribution of the latter species, but never in syntopy (Rubio and Gosá, 2010). Phenomena of allopatry by competition have been detected among *M. monspessulanus* and *H. viridiflavus* (Cortesogno, 1994; Naulleau, 1997), it being the competitive exclusion with *M. monspessulanus* that determines the southern boundary of the Iberian distribution of *H. viridiflavus* (Santos et al., 2010). For L. *bilineata*, the existence of competitive exclusion with *L. schreiberi* and *T. lepidus* has also been suggested, though more data are needed to confirm this (Delibes and Salvador, 1986; Gosá and Rubio, 2013). *R. dalmatina*, which has a possible Pleistocene record in Erralla (Esteban and Sanchiz, 1985), could be included in the same category as the above-mentioned species on account of its reduced Iberian distribution range (Gosá, 2002), bounded to the south of the Basque Country and northern Navarra, in contrast to its expansion in Italy and the Balkans. This could be due to competitive exclusion processes with *R. temporaria* (Riis, 1997).

In projections of the current area of potential habitability for these four species in the Iberian Peninsula (Araújo et al., 2011), the potential viability of *R. dalmatina* is proposed along the Cantabrian fringe, in the northern half of Portugal and the western and central Pyrenees, where the potential area of *R. dalmatina* habitability overlaps with the distribution of *R. temporaria*. The same area of potential habitability is attributed to *L. bilineata*, where one of its possible Iberian ecological opponents is also located, the northwestern Iberian endemism L. *schreiberi*. For this latter lizard an area of potential habitability is proposed that ranges from the Basque Country to Catalonia through the Pyrenees and the southern pre-Pyrenean valleys, the two ends of the Pyrenees being occupied by *L. bilineata*. This reinforces the hypothesis of competitive exclusion between the two species of the genus *Lacerta*. By contrast, *Z. longissimus* and *H. viridiflavus*, which share roughly the same potential habitability area as *L. bilineata* and *R. dalmatina*, only come into direct conflict with *Z. scalaris* and *M. monspessulanus* in the Atlantic fringe that runs from the southern half of Galicia to the river Tagus.

However, it should be noted that Araújo et al. (2011) only include climate data for the Iberian populations in making their projections of potential distribution. Hence, it is possible that the potential habitability of *L. bilineata*, *Z. longissimus* and *H. viridiflavus* in Iberian Mediterranean regions has been underestimated due to the apparent Euro-Siberian affinities of these species in Iberia, when in fact they are species capable of living in much warmer areas in the other southern European peninsulas. For this reason, the hypothesis cannot be ruled out that the southern limits of their distributions are due to direct competition with *T. lepidus*, *Z. scalaris* and *M. monspessulanus*, respectively.

5. Conclusions and future prospects

In all 58 Iberian archaeo-paleontological sites with a herpetofaunal presence from the latest Pleistocene to the Late Holocene a total of 47 different taxa have been identified at generic and specific level. These are grouped taxonomically into eight urodelans: *P. waltl*, *S. salamandra*, *T. pygmaeus*, *T. marmoratus*, *I. alpestris*, *C. asper*, *C. lusitanica* and *L. helveticus*; 12 anurans: *A. obstetricans*, *A. cisternasii*, *D. galganoi*, *P. cultripes*, *B. spinosus*, *B. calamita*, *R. temporaria*, *R. dalmatina*, *R. iberica*, *P. perezi*, *P. punctatus* and genus *Hyla*; three chelonians: *M. leprosa*, *E. orbicularis* and *T. hermanni*; one amphisbaenian: *B. cinereus-mariae*; one iguanian: *C. chamaeleon*; one gecko: *T. mauritanica*; one anguimorph: *A. fragilis*; two skinks: *C. bedriagai* and *C. striatus*; five lizards: *A. erythrurus*, *P. algirus*, *T. lepidus* and genera *Lacerta* and *Podarcis*; and 13 snakes: *N. maura*, *N. natrix* sensu lato, *C. austriaca*, *C. girondica*, *H. hippocrepis*, *Z. longissimus*, *Z. scalaris*, *H. viridiflavus*, *M. brevis*, *M. monspessulanus*, *V. aspis*, *V. seoanei* and *V. latastei*.

The fossil herpetofaunal assemblages allow us to establish two major biotic regions during the latest Pleistocene, albeit with ill-defined limits because of the current lack of a continuum of paleo-archaeological sites with a herpetological record between the two groups. The first biotic region is formed by the center and south of the Iberian Peninsula, with *B. calamita*, *B. spinosus*, *T. lepidus*, *Z. scalaris* and, to a lesser extent, *P. waltl*, *P. cultripes*, *T. hermanni*, *M. monspessulanus* and *V. latastei* as the most representative species of the herpetofaunal record. The second major biotic region comprises the Atlantic-Cantabrian facade and northeastern Iberia and is characterized by the association of *R. temporaria* and *A. fragilis* as the dominant species of the prehistoric sequences, although in the northern area they are accompanied by *B. spinosus*, *B. calamita* and the genera *Alytes* and *Vipera* as the most representative taxa, while in the northeastern Iberian record they are accompanied by *A. obstetricans*, *B. calamita*, *B. spinosus*, *P. punctatus* and *C. girondica* as the dominant species.

The paleoclimatic implications of these large associations indicate the maintenance of typically dry Mediterranean conditions in the central and southern regions, while the northern and northeastern areas present a generally mild and humid climatic regime dominated by wooded spaces and wet meadows. However, this scenario may be affected by the possible bias of a record with widely scattered sites in the south and center of the Iberian Peninsula, and the absence of published herpetofaunal assemblages for MIS 2 of the northeastern area. New discoveries and publications, which may fill the gaps in the different regional records, will confirm or challenge these observations.

The main biogeographic changes occur after the beginning of the postglacial phase, with the resulting climate improvement that produced the expansion of the thermophilic species towards the north of the Iberian Peninsula, possibly taking advantage of the existence of natural corridors such as the Ebro Valley or the Atlantic coast. In parallel, new Italian species entered via the Pyrenean margins having passed through southern France; their expansions may have been halted in the north by the contemporaneous colonization of Iberian Mediterranean species from the south. The introduction of various Maghrebian species, possibly caused by humans and dated by genetic studies to relatively recent times, represents the most recent processes of emergence and expansion of new amphibians and reptiles in the Iberian Peninsula during the Middle-Late Holocene.

New prospects are also opened up for increasing our knowledge of the herpetofauna reported in archaeological sites from cultural phases that saw the rise of a sedentary human lifestyle and the spread of agriculture and husbandry, i.e., from the Neolithic period. Increased attention to the archaeo-herpetological record of this chrono-cultural phase, in which the human impact and pressure on the landscape increased, will enable us to see how species of amphibians and reptiles adapt to anthropic changes in the environments near human settlements and to the newly generated ecological niches, even within the settlements themselves, ascertaining whether such changes help or impede the appearance of these species in the zooarchaeological record. Also of special interest are future studies of the records from those periods that saw an intensification of cultural and commercial contacts with other Mediterranean regions, from the Neolithic to the arrival of Phoenician and Greek settlers and traders in the Iron Age or the establishment of the Roman dominion in the Iberian Peninsula. These movements of people, ships and goods have been linked with the possible introduction, intentional or not, of herpetofauna from other regions, a phenomenon that still occurs today though on a global level, bringing the problem of alien and invasive species that enter the natural environment, exemplified by the case of *Trachemys scripta* in present-day Iberia.

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Appendices A, B & C. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2017.06.010.

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Elucidating anuran accumulations: massive taphocenosis of tree frog *Hyla* from the Chalcolithic of El Mirador cave (Sierra de Atapuerca, Spain)

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ABSTRACT

Anurans, such as frogs and toads, are occasionally very abundant in archaeo-paleontological sites and representing > 80% of the remains. These accumulations have been linked mainly to human consumption in the European context, by the preferential selection of body parts and by the presence of burning, and to a lesser extent, cut marks (as in Chalain 3, Baume d'Ogens, Kutná Hora-Denemark). However, there are also records of accumulations attributed to natural catastrophic events (Bois-Roche). This research presents a taphocenosis of microvertebrates of reduced dimensions (7.8 × 2.7 × 2.4 cm) containing 2526 bones, from El Mirador cave of Atapuerca (Burgos, Spain) contemporaneous to an adjacent Chalcolithic burial (ca. 4500 BP). The taxonomical study has identified at least 12 different taxa, which include one urodele, two anurans, seven squamates and two rodents. Tree frogs, *Hyla* gr. *arborea* (*Hyla molleri*), constitutes 84% of the assemblage. Quantitative and qualitative taphonomic analyses are focused on *Hyla* bones and show the presence of breakage and digestion marks associated with animal predation, albeit in low percentages and in light or moderate degrees. Due to its characteristics, El Mirador accumulation has been identified as a pellet accumulation produced by a medium-large owl (category 2). The nocturnal raptor hunted its preys during a wet period in spring, when the reproduction of the tree frogs occurs, showing a possible evidence of opportunistic predation on a seasonal resource. These findings help to understand the importance of anurans in the trophic chains of Prehistoric times, not only among human groups but also among non-human predators.

1. Introduction

Amphibians are one of the least studied groups in the Quaternary fossil record, due to the lack of specialists, in comparison to other groups as the small mammals. Nevertheless, the discoveries and publications of the last decades are beginning to increase our knowledge about them. Anuran (as frogs and toads) occasionally appear in large accumulations or taphocenoses that are formed exclusively or almost entirely by a single species (e.g., Bailon, 1997; Blain and Villa, 2006). The Early Pleistocene and Middle Pleistocene sequences of the Atapuerca sites (Burgos, Spain) are good examples, where some anuran species are abundant in certain levels. This is the case of the toad *Epidalea calamita* in Gran Dolina cave of Atapuerca, the record of which accounts for 70% of all amphibian individuals during the Early-Middle Pleistocene (Blain, 2005; Blain et al., 2008).

Kyselý (2008) proposes five hypotheses to explain anuran accumulations in archaeological records: 1) mortality during hibernation/aestivation, 2) natural traps, 3) non-human predation, 4) human consumption, and 5) ritual human activities. Other documented causes are catastrophic mortality, such as floods (Cochard, 2004), as well as the ethological troglophily and trogloxeny of many species of European amphibians (Montori and Martínez-Silvestre, 2015). Human consumption has generated a significant number of archaeological records in the European context, from the Mesolithic to the Chalcolithic periods, with historical and ethnographic records that extend to the present day (Bailon, 1997; Hüster, 2004; Chiquet, 2005; Kyselý, 2008). They are

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located within habitation sites, both in sedentary contexts, mainly towns as Seeberg Burgäschisee-Süd (Boessneck et al., 1963), Chalain 3 (Bailon, 1997), Arbon Bleiche (Hüster, 2004), and Kutná Hora-Denemark (Kyselý, 2008), or in temporary settlements of hunter-gatherer societies as Baume d'Ogens cave (Chiquet, 2005).

The sequence of El Mirador cave in Atapuerca, whose excavation is still ongoing, has yielded a large amount of microvertebrate bones (> 100,000), although only the small mammal record has been published to date (López-García, 2008; Bañuls-Cardona et al., 2013, 2017a,b). Twenty concentrated accumulations containing microfaunal remains with a significant abundance of herpetofauna were found in the levels from the Chalcolithic to the Bronze Ages (MIR5 and MIR4). To determine their origin, a taphonomic analysis was performed on the major accumulation (MIR5-P21-n4), identified as a small taphocenosis with a high number of remains (2,526), mostly belonging to anuran amphibians (84.91% of NME).

Additionally, this accumulation was compared with other taphocenoses from the Late Pleistocene level of Bois-Roche cave (Cochard, 1998, 2004), the Neolithic settlement of Chalain 3 (Bailon, 1997), and the Chalcolithic site of Kutná Hora-Denemark (Kyselý, 2008). These three sites have yielded some of the largest accumulations of anurans in the European archaeological context and provide a comparative context with which to infer new perspectives about amphibian taphonomy. The amphibian assemblage from the Neolithic level of El Harhoura 2, a karstic cave on the western Atlantic coast of Morocco, has also been included (Stoetzel et al., 2008,2010, 2011, 2012).

Currently, there is a lack of actualistic references on amphibian taphonomy and herpetological taphonomy in general. The modern references about non-human predation are limited by the low number of anuran remains and pellets/accumulations or by the predator (mainly, the common barn owl *Tyto alba*) in the available literature (e.g., Pinto Llona and Andrews, 1999; Rey and Sanchiz, 2005; Denys et al., 2018). Despite this, they are included in the Discussion.

2. El Mirador cave

El Mirador cave (*Cueva de El Mirador*) is located on the slopes of the southern tip of the Sierra de Atapuerca, within the municipality of Ibeas de Juarros, as part of the Atapuerca karst system. It is located at 42° 20′ 58″ N and 03° 30′ 33″ W and it rises to 1033 m.a.s.l. (Fig. 1) over the middle basin of the Arlanzón River. The cave is currently 23 m wide by 4 m high and 15 m deep, and is configured as an open shelter due to the collapse of the vault (Vergès et al., 2002).

Between 1999 and 2008, the archaeological work focused on a 6 m^2 test pit located in the central area of the western half of the cave, where a large Holocene succession was found, composed of 24 differentiated archaeological levels (Fig. 1): Levels MIR1 and MIR2 are mixed layers formed by animal burrows and modern anthropogenic actions; MIR3 is partially disturbed, with mixed remains from the Middle to Late Bronze Age; MIR4 is a substantial level from the Middle Bronze Age, which includes at its base a secondary burial of cannibalised human bones from the Early Bronze Age that were buried during the Middle Bronze Age (Cáceres et al., 2007; Vergès et al., 2016); MIR5 is a thin level with scarce anthropogenic contributions, but it is rich in small vertebrate remains (Vergès et al., 2002). The remaining Holocene levels (MIR6-24) are assigned to the Neolithic and are mostly made up of livestock pen waste, mainly *fumiers*, with the Late Neolithic represented in the top of the sequence (including MIR6) (Angelucci et al., 2009; Vergès et al., 2008, 2016).

MIR5 correspond to a phase of abandonment of the cave's use for livestock and represents a hiatus of one thousand years, between the Late Neolithic and the Bronze Age (Vergès et al., 2002), which possibly places it as contemporaneous with the Chalcolithic burial in MIR203 (4,880–4,390 cal. BP) (Ceperuelo et al., 2014, 2015; Lozano et al., 2015; Vergès et al., 2016).

3. Material and methods

3.1. Sampling

During the 2000 excavation campaign in El Mirador cave, a cylindrically shaped concentrated accumulation (7.8 cm in length, 2.7 cm in width and 2.4 cm in height) was identified containing sub-fossil microvertebrate remains on the roof of level MIR5 (z: 1284) and in grid P21 of the central test pit. This taphocenosis was isolated, its location was recorded, and it was removed. The bone remains were subsequently obtained in the micropaleontology laboratory of the Catalan Institute of Human Paleoecology and Social Evolution (IPHES) through screening with a running-water washing system and decreasing mesh sizes (5 mm, 2 mm and 0.5 mm).

3.2. Taxonomic identification

The following elements were used to identify the herpetofauna: parasphenoid, frontal, humerus and vertebrae for caudates (Buckley and Sanchiz, 2012; Gleed-Owen, 1998; Ratnikov, 2015) and frontoparietal, squamosal, scapula, humerus, vertebrae and ilium for anurans (Bailon, 1999; Blain and Arribas, 2017), maxilla, pteryoid, frontal, parietal, quadrate, coronoid, dentary and vertebrae for non-ophidian squamates (Anguidae, Scincidae, Lacertidae) (Barahona and Barbadillo, 1997; Blain, 2009; Caputo, 2004; Barahona, 1996; Gleed-Owen, 1998), and vertebrae for snakes (Szyndlar, 1984). For the small mammals, the first lower molar for Arvicolinae and isolated teeth for *Apodemus sylvaticus* (Chaline, 1972; Cuenca-Bescós et al., 1997, 2008) were used. Modern specimens from the reference collections of the Museo Nacional de Ciencias Natural of Madrid (MNCN-CSIC) and the IPHES have been used as comparison material.

The sexual determination of the anurans was based on the morphology of the humerus. The presence of a developed mesial crest in the distal part was used as a diagnostic character of the male sex, as opposed to its lower development in females (Bailon, 1999).

3.3. Anatomical representation

The minimum number of elements (MNE) was estimated from the total number of each element, specially the diaphysis. Among the fragmentary bones, the proximal-diaphysis-distal fragments were combined and counted as a single element. In the case of *Hyla* gr. *arborea*, the percentage of representation (PR) of each anatomical element was calculated according to that proposed by Dodson and Wexlar (1979), which compares the observed quantity for each element versus the total expected amount:

$$PR = \frac{MNEi}{SAi \times MNI}$$

in which the minimum number of elements of each element (MNEi) is divided by the product of the multiplication of the specific amount (SAi) of each considered bone in a single individual by the minimum number of individuals (MNI) of *Hyla* gr. *arborea*.

Anatomical proportions were evaluated based on the following indices, adapted from Andrews (1990) and Cochard (1998):

The index of representation of the postcranial skeleton in contrast to cranial skeleton:

$$PC/C = \frac{MNE\,[humeri + radioulnae + femora + tibiofibulae]}{MNE\,[the\ most\ represented\ cranial\ bone + angular]} \times \frac{4}{8} \times 100$$

where *4/8* is the correction to compensate the difference in EA between the compared bones.

The index of representation of the elements of the forelimbs in comparison with elements of the hindlimbs:

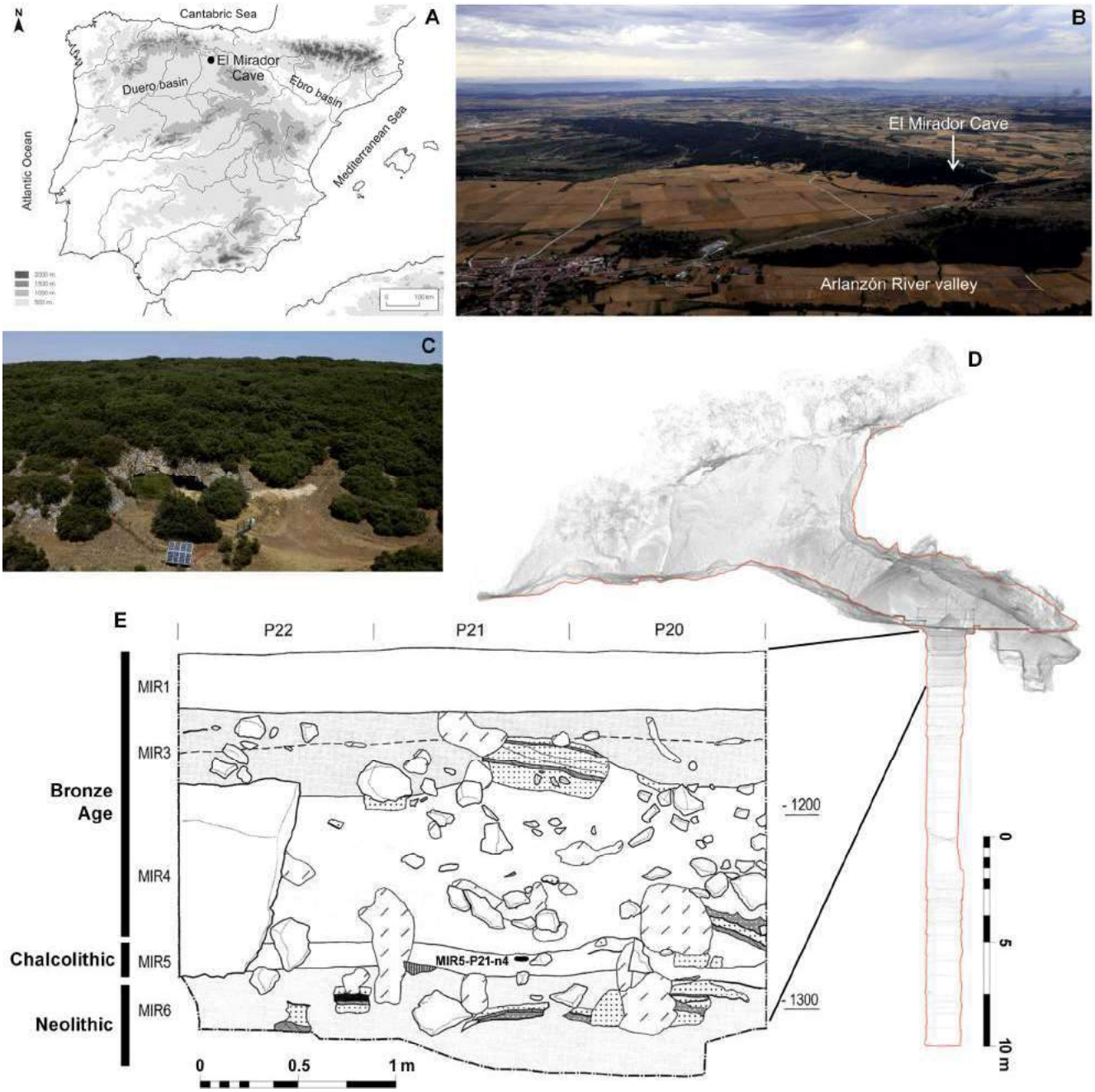

Fig. 1. El Mirador cave from Sierra de Atapuerca (Burgos, Spain). A: Location of El Mirador cave in the Iberian Peninsula; B-C: aerial views of El Mirador cave; D: N-S section of the cave with the test pit; E: stratigraphic profile from the Late Neolithic-Bronze Age south section of the test pit and the position of the MIR5-P21-n4 studied accumulation.

$$FL/HL = \frac{MNE\,[humeri + radioulnae]}{MNE\,[femora + tibiofibulae]} \times 100$$

And the index of representation of the distal elements compared to the proximal elements of the extremities:

$$D/P = \frac{MNE\,[radioulnae + tibiofibulae]}{MNE\,[humeri + femora]} \times 100$$

3.4. Digestion and breakage

The taphonomic study is based on the methodology established by Andrews (1990) and adapted for amphibians by Pinto Llona and Andrews (1999), with contributions from Stoetzel et al. (2012) and Fernández-Jalvo and Andrews (2016), as well as the observations made on the studied sample and modern owl pellets (Fig. 2). The degree of digestion has been classified into four grades (grade 0 – none, grade 1 – light, grade 2 – moderate, and grade 3 – heavy) based on the condition of the following modifications:

1) Rounding by the action of gastric acids on the sharp edges of the fractured bones before digestion. Initially it presents a slight smoothing over the fractures (1 – light), which as it increases, generates a greater rounding and polishing of the edges (2 – moderate) until the formation of very rounded and polished profiles (3 – heavy).
2) Cracking due to longitudinal fractures on the weakest parts of the bone element, mainly in the bone ends (1 - light), which can

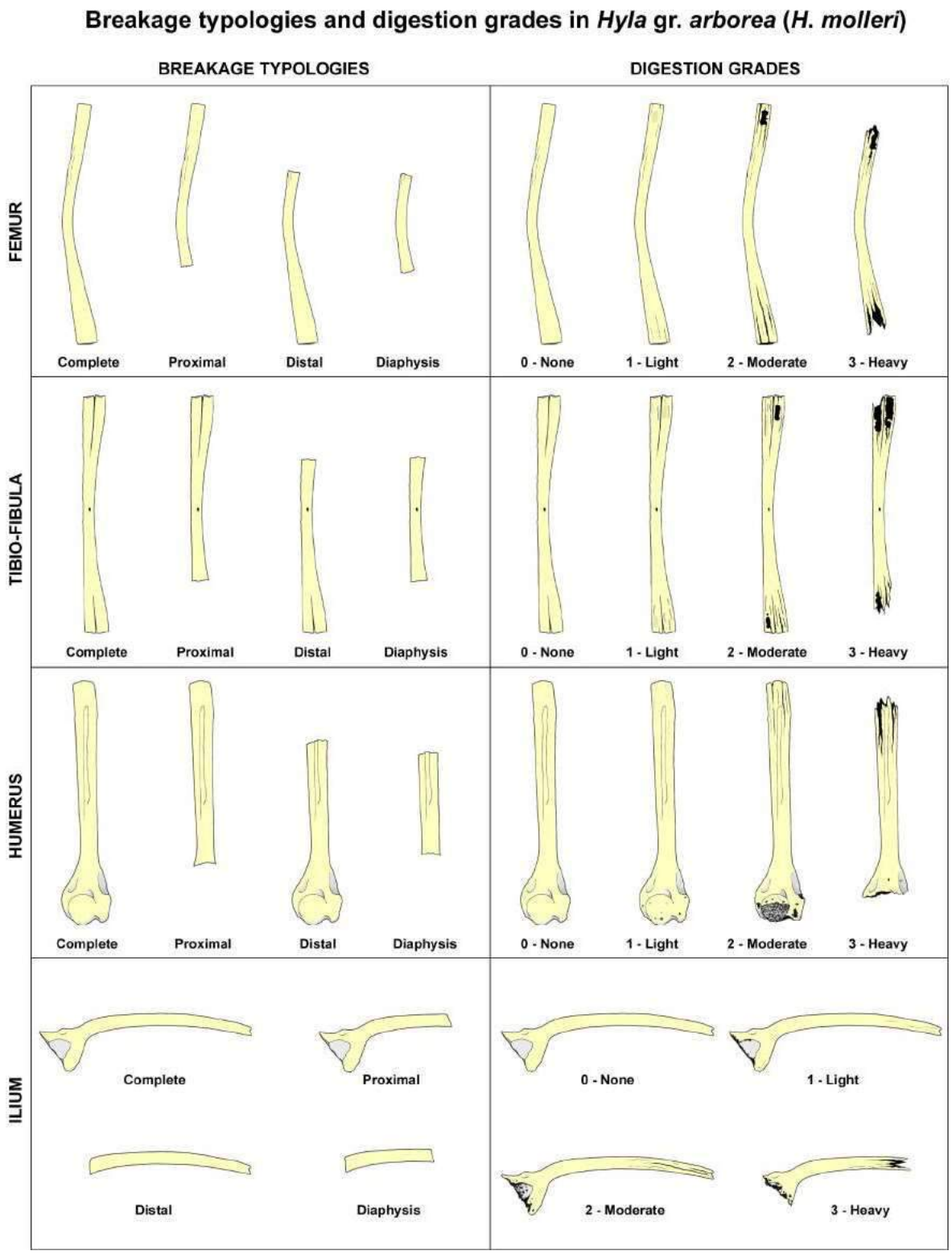

Fig. 2. Breakage typologies and digestion grades in *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave. The digestion grades represent the main digestive marks in the studied sample (splitting, thinning and bone collapse, and corrosion).

increase in length and width (2 – moderate) until it causes loss of the bone wall along the previous longitudinal lines (3 – heavy).

3) Thinning and plasticity of the bone walls, which to a greater degree can progressively produce a bowing towards the interior (1 – light), the collapse and the loss of sectors of the bone wall (2 – moderate) that extends through the bone as the digestion increases (3 – heavy).
4) Flaking by desquamation or exfoliation of the bone layers that can affect at surface level or the whole structure of the bone. Mostly this appears at the extremes of the bones or at the edges of the fractures, where small flakes are formed (1 – light), which at a more advanced stage increase the affected area and separate the different layers of the bone tissue (2 – moderate) and finally can generate the loss of the outermost layers and the exposure of the internal tissues (3 – heavy).

5) Digestive corrosion that causes the progressive bone loss of the articular regions. In the first phase, small holes are produced in the more porous parts of the articular surfaces, primarily on the distal humerus and proximal ilium (1 – light). A higher degree of digestion increases the size of these holes and the internal cancellous tissue is exposed (2 – moderate), until most of the articular regions are lost due to corrosion (3 – heavy).

The different typologies of breakage refer to the conserved part of the element after the fracture associated to the predation: e.g., "proximal" means that the bone preserves the proximal part, including the diaphysis, but it has lost the distal part due to the breakage (Cochard, 1998). In Pinto Llona and Andrews (1999) have been established four grades to analyse the breakage, where grade 0 refers to any element that has conserved its proximal, diaphysis and distal parts, and grade 3 refers only to the preservation of the most compact part of the bone, with grades 1 and 2 in between but without a further description. In this article, grade 1 corresponds with the incipient loss on the parts, specially on the bone ends, up to 25% of its total length; and grade 2 corresponds to a comparatively greater but moderate loss, with the fracture of one or both parts, up to a maximum of 50% of the total length (Fig. 3). Both terminal articular epiphyses femur and tibio-fibula, and the proximal articular epiphysis of the humerus have not been included in the fracture analyses because of their porous tissue and weak structure, which may be affected by other conservation biases. Microscope pictures were taken with the ESEM (environmental scanning electron microscope) at Rovira i Virgili University (URV), Tarragona.

4. Results

4.1. Faunal list

In total, 2542 skeletal remains were registered in the taphocenosis MIR5-P21-n4, with a MNE of 2035, which have been identified osteologically and assigned to the taxonomic level. They correspond to a MNI of 84, belonging to 12 different taxa, which include one urodele, two anurans, seven squamates and two rodents (Figs. 4 and 5, Table 1).

The predominant taxon is *Hyla* gr. *arborea*, with 1706 remains belonging to a minimum of 66 individuals, corresponding to 83.83% of the identified MNE in the sample and 78.58% of the total MNI (Fig. 5). The sexual determination of the *H.* gr. *arborea* individuals, based on the morphology of the humerus, establishes the presence of a MNI of 34 males and 25 females over a total MNI of 66. This shows a prevalence of males versus females in a ratio of 1.36:1, but no significative difference.

4.2. Hyla gr. arborea, skeletal representation

Of the taxa in the accumulation, the *H.* gr. *arborea* remains can be studied in the most detail. All the bones of this species have been documented, except the vomer, squamosal, frontal-parietal, supra-scapula, cleithrum and sternum (Table 2). These absences can be attributed to differential preservation, due both to their small size and delicate configuration, and to the partial or total cartilaginous composition of some of these bones, which do not undergo advanced ossification, thereby limiting their preservation. A similar problem has occurred with the metapodials and phalanges, since conservation and identification biases cannot be ruled out due to their fragility and small size. Because of this they have not been included in the representation analyses.

At the quantitative level, the most represented elements (PR > 80%) are the bones of the limbs (tibio-fibula, femur, and humerus), the pelvic girdle (ilium), shoulder girdle (scapula), and the vertebral region (dorsal vertebrae, sacral vertebra, and urostyle). In contrast, the most underrepresented elements (PR < 10%) are the clavicle, the maxilla and the pterygoid (Table 2). These three bones share a delicate configuration, with thin walls in contrast to the better-preserved elements, which are more massive and robust, again, possibly suggesting the occurrence of differential preservation in detriment to the more delicate elements.

According to the indices of anatomical representation (Table 3), proportionally there are twice as many postcranial bones than cranial elements in El Mirador accumulation. The distal long bones and proximal long bones are equally represented at the quantitative level, but there are fewer bones of the forelimbs than hindlimbs (82.47%).

4.3. Hyla gr. arborea, breakage and digestion

The percentage of breakage of the main long bones is low or very low in all analysed elements (Fig. 6B and C; Fig. 7). The femora exhibit less evidence of fracture losses, with a very high percentage of bones preserving their full length with marginal losses at the ends (Fig. 6B). In

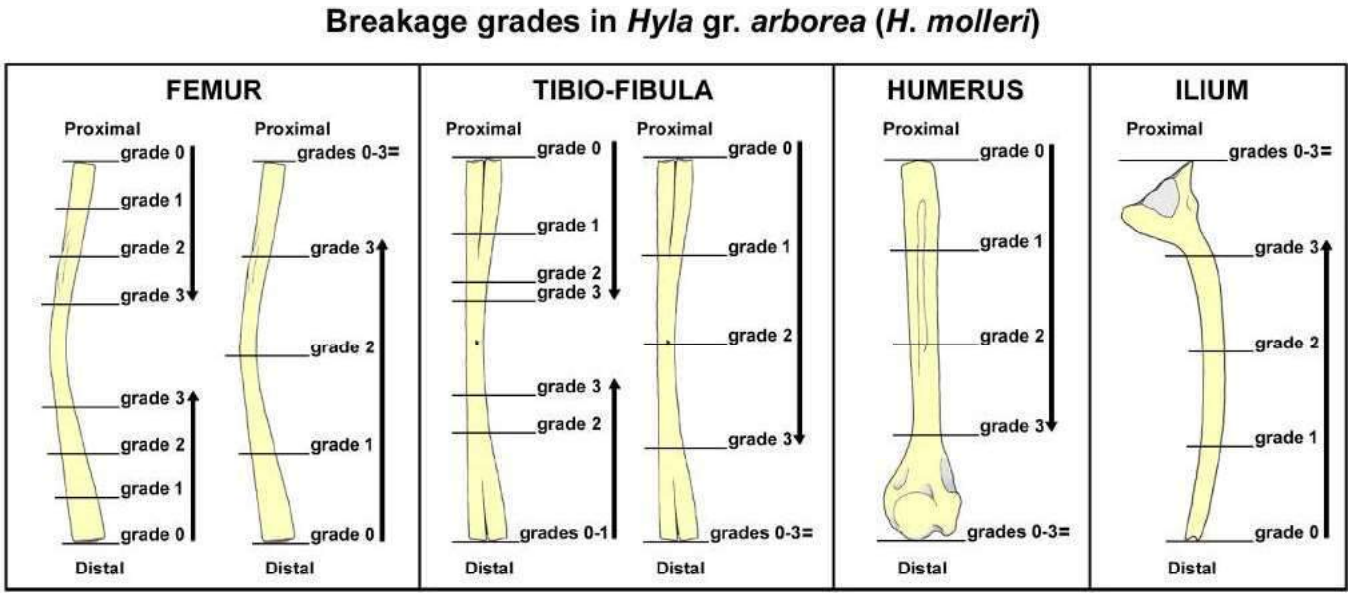

Fig. 3. Breakage grades in *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave. The arrows indicate the increasing breakage degree from one or both extreme parts (proximal and distal).

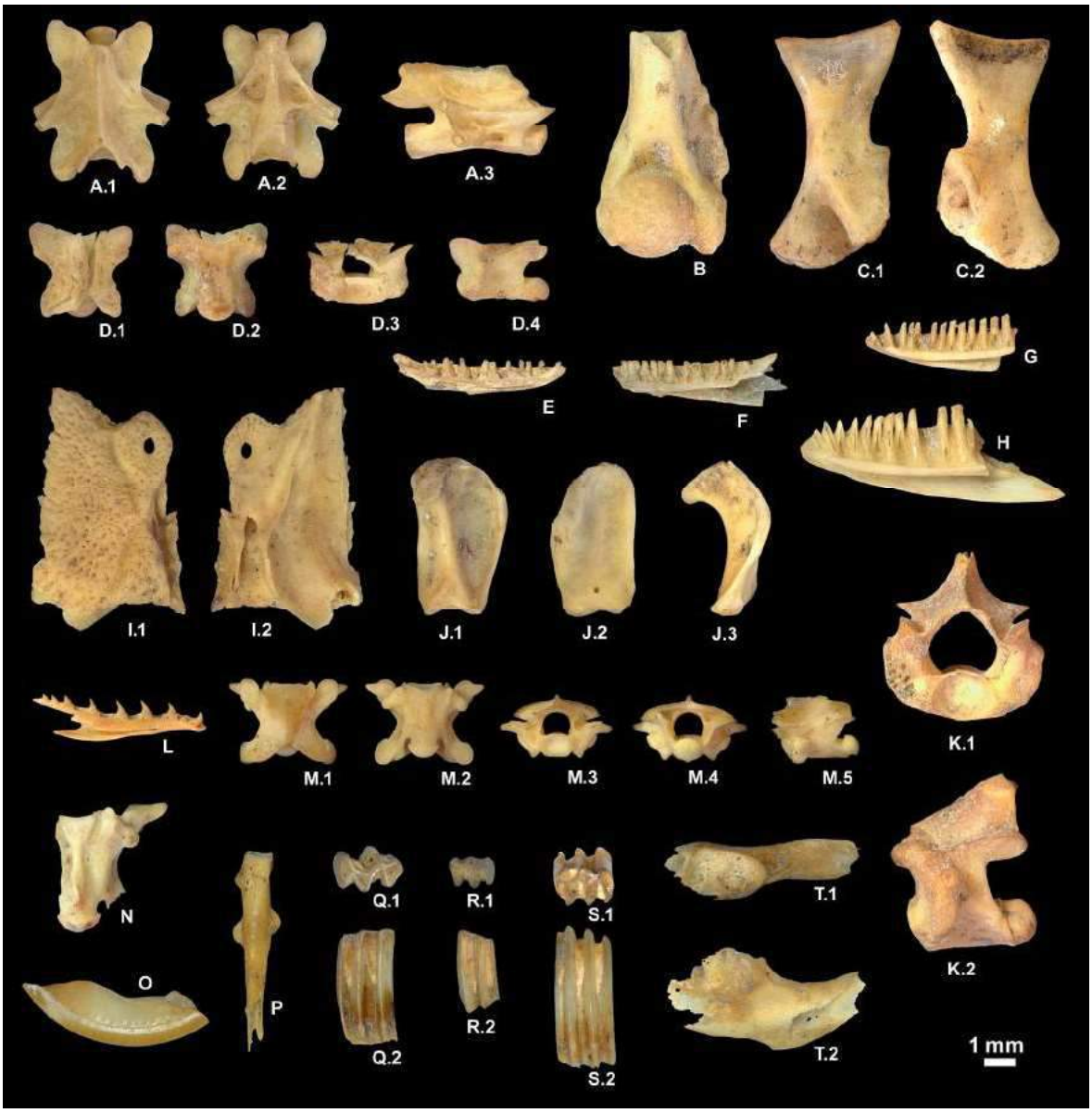

Fig. 4. Small vertebrates of the taphocenosis MIR5-P21-n4 from El Mirador cave. A: *Triturus marmoratus*, trunk vertebra, dorsal (A.1), ventral (A.2) and right lateral (A.3) views; B-C: *Rana temporaria*, B: right humerus, ventral view, C: right scapula, ventral (C.1) and dorsal (C.2) views; D: *Anguis fragilis*, trunk vertebra, dorsal (D.1), ventral (D.2), left lateral (D.3) and anterior (D.4) views; E-F: *Chalcides striatus*, E: left dentary, medial view; F: right dentary, medial view; G: Lacertidae indet. (small size), right dentary, medial view; H-J: *Lacerta* cf. *bilineata*, H: right dentary, medial view; I: parietal, dorsal (I.1) and ventral (I.2) views; J: quadrate, anterodorsal (J.1), posterodorsal (J.2) and lateral (J.3) views; K: *Timon* cf. *lepidus*, cervical vertebra, anterior (K.1) and left lateral (K.2) views; L-M: *Coronella austriaca*, L: left dentary, medial view; M: trunk vertebra, dorsal (M.1), ventral (M.2), anterior (M.3), posterior (M.4) and left lateral (M.5) views; N: *Vipera* sp., trunk vertebra, ventral view; O-P: Rodentia indet., left upper incisive, labial view; P: left ulna, posterior view. Q-S: Arvicolinae indet., Q: right upper molar (M2), occlusal (Q.1) and labial (Q.2) views; R: left upper molar (M3), occlusal (R.1) and labial (R.2) views; S: right upper molar (M1), occlusal (S.1) and lingual (S.2) views; T: *Apodemus* cf. *sylvaticus*, right mandible, occlusal (T.1) and labial (T.2) views.

contrast, the ilia are the most affected bones, with almost all fractures concentrated in the loss of the anterior projection (25.6%), and a low percentage of breakage loss in the articular area of the acetabulum (1.6%), the most compact part of the bone. The humeri and the tibio-fibulae have similar percentages of loss on their proximal extremes (11.45–12.28%). They differ in the low percentage of fracture at the distal end of the humeri (5.26%), which involves the loss of the condyle and the epicondyles, while the tibio-fibulae show a low percentage of fracture loss on both extremes, only preserving the diaphyses (6.11%) (Fig. 7).

The most affected element by digestion is again the ilium, with 46.6% bearing gastric alterations, while the least affected is the tibio-fibula (15.27%) (Fig. 7). The main alterations consist of longitudinal splits along the anterior projection and, to a lesser extent, corrosions in the area of the acetabulum and in the joint region with the ischium-pubis (Fig. 6G). In the humeri, corrosions appear mainly in the condyle area, where the bone is more porous and permeable to the action of stomach acids during digestion (Fig. 6H-I). The longitudinal splits are circumscribed mainly to the proximal half of the humerus diaphysis. Digestion marks are concentrated in the long bones of the hindlimb at its distal and proximal ends. Long splits appear in the femora and tibio-fibulae, as does loss of bone mass due to thinning, in the heavier cases with partial inwards curving and collapse (Fig. 6D-F). This type of gastric alteration is absent in the humeri and ilia, possibly due to the different configuration of these bones, which are more porous and internally compact in their joint areas.

Fig. 5. *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave. A: left premaxilla, medial view; B: left maxilla, medial view; C: parasphenoid, ventral view; D: right pterygoid, dorsal view; E: right angular, dorsolateral view; F: atlas, anterior view; G: anterior trunk vertebra, dorsal (G.1) and anterior (G.2) views; H: posterior trunk vertebra, dorsal view; J: urostyle, dorsal view; K: right coracoid, dorsal view; L: right clavicle, dorsal view; M: left scapula, dorsal view; N: male right humerus, ventral view; O: left radio-ulna, ventral view; P: femur, lateral view; Q: tibio-fibula, ventral view; R: left tarsus with articular epiphyses, ventral view; S: isquion-pubis, posterior view; T: right ilium, lateral view.

Table 1
Taxonomic attribution, minimum number of identified elements (MNE), and minimum number of individuals (MNI) of the taphocenosis MIR5-P21-n4 from El Mirador cave (Atapuerca, Spain).

	Taxa	MNE	MNE%	MNI	MNI%
Amphibians	*Triturus marmoratus*	36	1.77	3	3.57
	Hyla gr. arborea (molleri)	1,706	83.83	66	78.58
	Rana temporaria	22	1.08	1	1.19
Squamates	*Anguis fragilis*	12	0.59	1	1.19
	Chalcides striatus	2	0.10	1	1.19
	Lacertidae indet. (small size)	24	1.18	1	1.19
	Lacerta cf. *bilineata*	93	4.57	3	3.57
	Timon cf. *lepidus*	2	0.10	1	1.19
	Coronella austriaca	110	5.41	2	2.38
	Vipera sp. (*aspis/seoanei*)	3	0.15	1	1.19
Mammals	Rodentia indet.	16	0.79	–	–
	Arvicolinae indet.	8	0.39	3	3.57
	Apodemus cf. *sylvaticus*	1	0.05	1	1.19
Total		2,035	100	84	100

In general, the coincidence of two different digestion marks in a single element is rare, and mainly consists of splitting with gastric corrosion in ilia (1.6%) and humeri (5.26%) and splitting with thinning in femora (0.83%) and tibio-fibulae (0.76%) (Fig. 6E). Only tibio-fibula displays rounding on the fracture edges (0.76%) which have been identified and associated with digestion (Fig. 6C). Another taphonomic agent not associated with predation that has been documented is the possible action of roots on one femur, causing grooves over the external surface and a small perforation (Fig. 6A).

According to the criteria established by Pinto Llona and Andrews (1999) on anurans remains, the MIR5 assemblage corresponds to a breakage category 2, because most of the bones are complete, and a digestion category 2, because the effects of digestion are relatively low in degree and percentage (Table 4, Fig. 7).

4.4. Taphonomy of the remaining taxa

The bones of the other taxa represented in the accumulation exhibit a low percentage of breakage and/or digestion. The high degree of breakage of the larger elements stands out, such as the dentaries, frontals and parietals of the lizards (*Lacerta* cf. *bilineata* and *Timon* cf. *lepidus*) (Fig. 3H, and I), and the tibio-fibulae and humeri of *Rana temporaria* (Fig. 4B). However, other smaller elements are mostly intact, such as the vertebrae of *Coronella austriaca* and *Triturus marmoratus* (Fig. 3A, and M). The strongest evidence of digestion is visible in the dorsal vertebrae of *Anguis fragilis*, with cracks following lines of weakness (Fig. 4D.1); in the vertebra of *Timon* cf. *lepidus*, with partial loss due to corrosion in the right synapophysis and neural spine (Fig. 4K.1); as well as in the proximal region of the right scapula of *R. temporaria* (Fig. 4C.1). Another digestion alteration is the rounding of the fracture edge in the diaphysis of the right humerus of *R. temporaria*

Table 2
Quantification of the minimum number of elements (MNE), the specific amount (SA) of each bone in a single individual, the expected number of elements from the total representation according to the minimum number of individuals (MNI = 66), and the percentage of presentation (PR), at the level of each bone and anatomic regions, in *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave.

	MNE	SA	Expected	PR
Skull bones				**29.11%**
Premaxilla	11	2	132	8.33%
Maxilla	48	2	132	36.36%
Sphenethmoid	25	1	66	37.88%
Parasphenoid	19	1	66	28.79%
Pterygoid	12	2	132	9.09%
Prootic-exoccipital	92	2	132	69.70%
Angular	18	2	132	13.64%
Vertebrae				**76.55%**
Atlas	39	1	66	59.09%
Dorsal vertebrae	389	7	462	84.20%
Sacral vertebra	57	1	66	86.36%
Urostyle	53	1	66	**80.30%**
Shoulder girdle				**38.64%**
Clavicle	8	2	132	6.06%
Coracoid	38	2	132	28.79%
Scapula	107	2	132	81.06%
Forelimb				**78.41%**
Humerus	114	2	132	86.36%
Radio-ulna	93	2	132	70.45%
Pelvic girdle				**62.50%**
Ischium-pubis	20	1	66	30.30%
Ilium	125	2	132	94.70%
Hindlimb				**95.07%**
Femur	120	2	132	90.91%
Tibio-fibula	131	2	132	99.24%
Tarsus	187	4	264	**70.83%**
TOTAL	**1,706**		**2,838**	**60.11%**

(Fig. 4A).

Among the small-mammal remains, two Arvicolinae molars show evidence of digestion in the form of dissolution on the enamel edges: one with a light degree (Fig. 4Q) and the other with a moderate degree (Fig. 4R). The mandible fragment assigned to cf. *Apodemus* cf. *sylvaticus* presents traces of heavier digestion with loss of the posterior part (Fig. 4T). Other corrosion interpreted as light digestion were identified on a caudal vertebra, the scapula and on the proximal epiphysis of the ulna (Fig. 4P).

5. Discussion

5.1. Comparison with the archaeological record

The comparison between the taphocenosis MIR5-P21-n4 from El Mirador cave, dominated quantitatively by *H.* gr. *arborea*, with other significant accumulations of anurans in the European archaeological record has allowed us to establish differences with regard to their origins (Table 5, Fig. 8). The comparative analysis of PR for each element or anatomical group with those obtained in *P. punctatus* from Bois-Roche (Cochard, 1998, 2004), in *R. temporaria* from Chalain 3 n.VI (Bailon, 1997), and from Kutná Hora-Denemark F.36 (Kyselý, 2008) shows a similar pattern in the posterior part of the body of the anurans, with a very high PR for the hindlimbs (femora, tibio-fibulae), and partially for the ilia (Fig. 8). The accumulation from El Mirador cave presents higher values, significantly in the skull elements, vertebrae, scapulae, radio-ulnae, femora, and tarsi. The lowest PR values occur in the ischia-pubis (30.30%) and coracoids (28.79%), although these are relatively high values compared to the rest of the record. El Mirador shares the general tendency of very high PR values both in the ilia and in the bones of the hindlimbs, but differs from the other accumulations in the high PR of the forelimb bones (humeri and radio-ulnae) and scapulae.

These high percentages from El Mirador contrast with those exhibited in Chalain 3 n.VI ZB and Kutná Hora-Denemark F.36. Both accumulations present very low PR in almost the entire skeleton, except in the urostyle (9.80–26.71%), humerus (13.80–33.06%) and ilium (26–29.32%), but primarily in the femur (57.70–84.04%) and tibio-fibula (99.84–100%). In contrast, Chalain 3 n.VI ZA presents a very high PR of the urostyle (98.04%) and ilium (100%), but lower percentages for femur (68.45%), and significantly lower for tibio-fibula (65.69%). The Bois-Roche accumulation presents more moderate PR values, although it also has a substantial deviation towards higher PR values for the ilia and the hindlimbs. The predominance of the long bones of the hindlimbs versus the long bones of the forelimbs was observed in all accumulations, notably in Chalain 3 n.VI ZB and Kutná Hora-Denemark F.36 (19.49% and 8.04%, respectively), which also have an enormous predominance of postcranial elements over cranial bones (4496.67% and 4570%) (Table 3).

The archaeological sites bearing evidence of human consumption of the frog *R. temporaria*, like Mesolithic Baume d'Ogens (Chiquet, 2005), Neolithic Chalain 3 (Bailon, 1997), and Chalcolithic Kutná Hora-Denemark (Kyselý, 2008), are characterised by the high representation of the hindlimbs and pelvic girdle compared to any other skeletal part. This preferential representation of the hind parts of the frogs' body is related to its greater meat supply. This bias is significant, taking into account the PRs, in the taphocenosis of the ZB area of Chalain 3 n.VI and of pit 36 from Kutná Hora-Denemark, with a very high representation of the tibio-fibula (ca. 100%), while in Baume d'Ogens, the ilium is the most represented element in the accumulation. Similar representation patterns with predominance of the hindlimb bones of *R. temporaria* have also been identified in other sites, like in the Neolithic settlements of Motte-aux-Magnins from Clairvaux-les-Lacs (Jura, France) (Rage, 1989), Seeberg Burgäschisee-Süd (Solothurn, Switzerland) (Boessneck et al., 1963) and Arbon Bleiche (Thurgau, Switzerland) (Hüster, 2004).

Unlike in the ZB area, the accumulation of *R. temporaria* in the ZA area of Chalain 3 N.VI yielded PRs that are noticeably greater for the ilium, the urostyle and the humerus, which reach PRs very close or equal to 90–100%, and in general, greater PRs for the remaining bones that are underrepresented in the other area inside the site. According Bailon (1997) this has been explained by a functional difference between the two areas: ZA could have been the area where the frogs were processed, coinciding with the location of the central bonfire of the

Table 3
Percentage values of the anatomic representation indexes: postcranial elements (humerus, radio-ulna, femur and tibio-fibula) versus cranial elements (most represented element plus angular), distal long bones (radio-ulna and tibio-fibula) versus the proximal long bones (humerus and femur), and of the anterior long bones (humerus and radio-ulna) versus the long posterior bones (femur and tibio-fibula) in *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave (MIR5.4) compared with those obtained in *Pelodytes punctatus* from Bois-Roche (BR, Cochard, 1998), in *Rana temporaria* from Chalain 3 n.VI ZA. and Chalain 3 n.VI ZB (CH3 VI ZA and CH3 VI ZB., Bailon, 1997) and in *Rana temporaria* from Kutná Hora-Denemark F.36 (KH-D F.36, Kyselý, 2008).

	MIR5.4	B-R	CH3 VI ZA	CH3 VI ZB	KH-D F.36
Post-cranial vs. cranial	208.18%	158.97%	175.40%	4,496.67%	4,570.00%
Distal vs. proximal	95.73%	123.67%	60.07%	87.62%	167.25%
Forelimbs vs. hindlimbs	82.47%	69.47%	89.04%	19.49%	8.04%

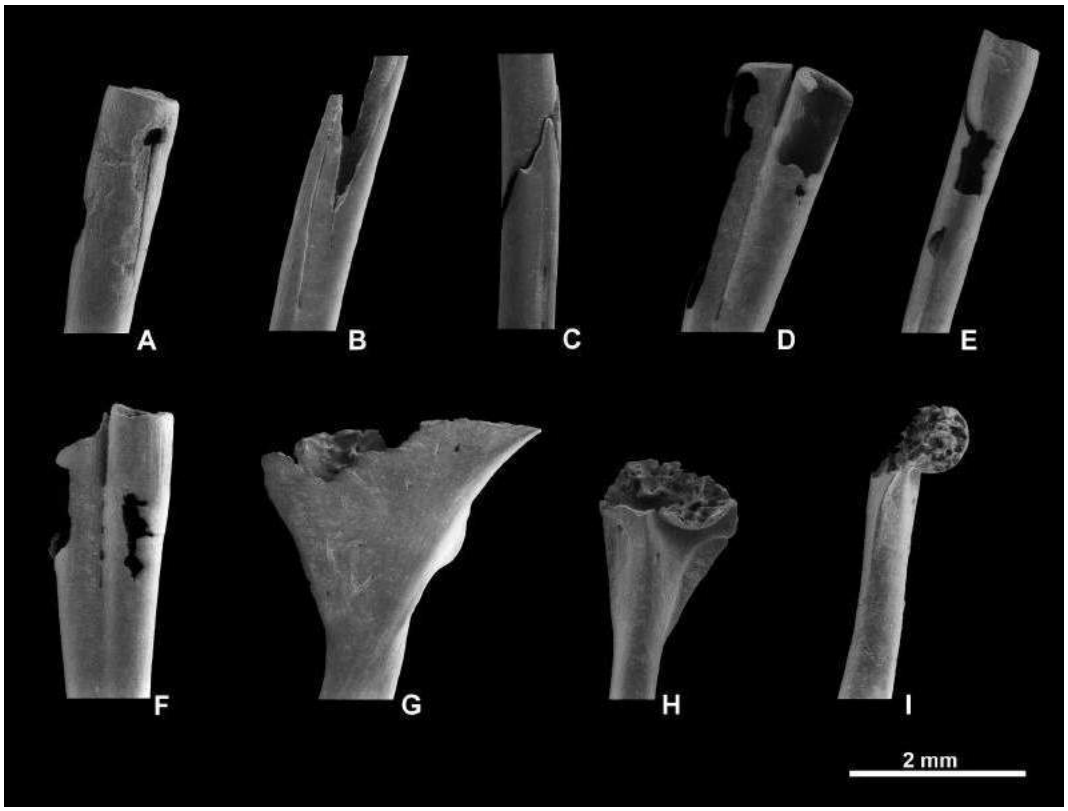

Fig. 6. Taphonomic marks on *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave: A) marks of roots on proximal femur; B) fractures on proximal femur; C) light rounding on fracture edges on the diaphysis of tibio-fibula; D) Moderate thinning and bone collapse on distal tibio-fibula; E) moderate thinning and bone collapse and light splitting lines on proximal femur; F) thinning, bone collapse and splitting lines on distal tibio-fibula; G) moderate corrosion on proximal ilium; H) and I) moderate corrosions on distal humeri.

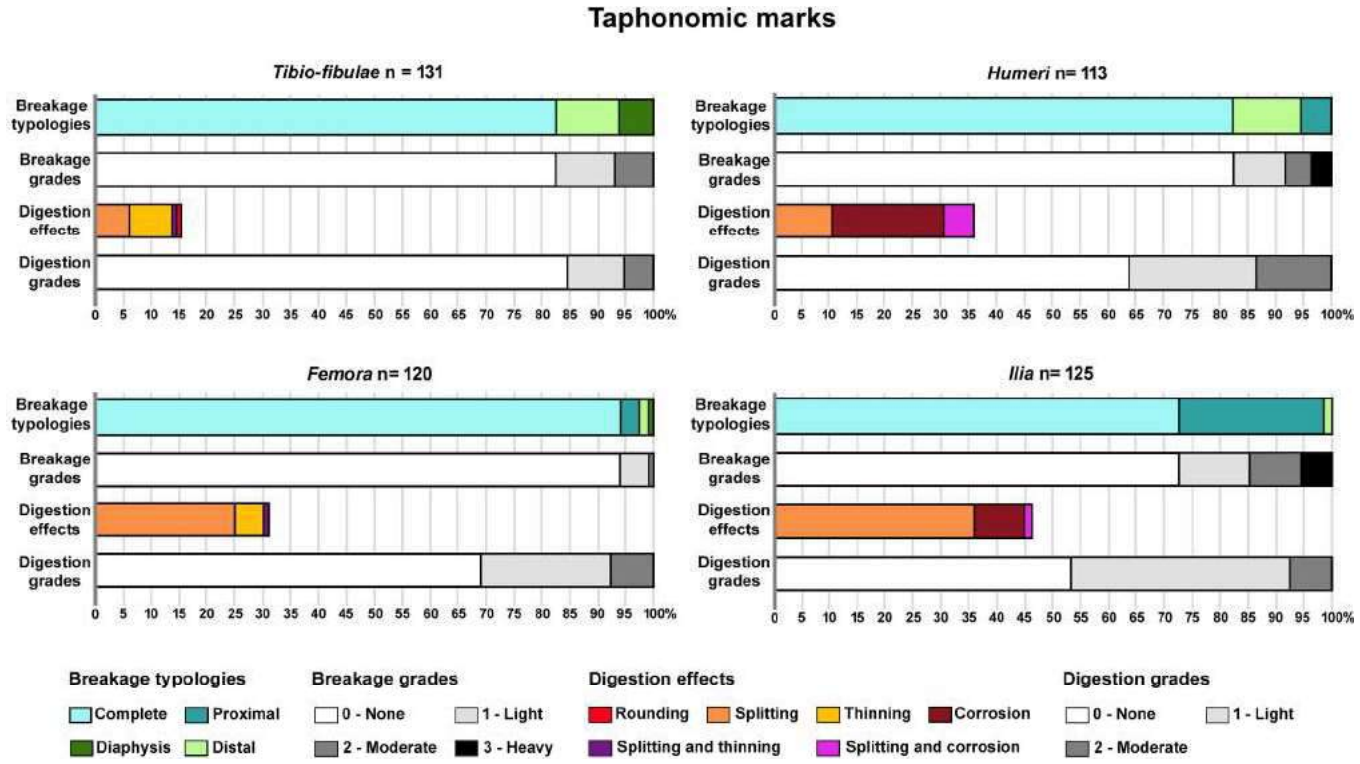

Fig. 7. Distribution and grades of the breakage, and effects and grades of digestion in the main long bones (humerus, femur, tibio-fibula and ilium) of *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave.

Table 4
Percentages according to grades of breakage and digestion in *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave.

Percentage of breakage (%)	Humeri n = 114	Ilia n = 125	Femora n = 120	Tibio-fibulae n = 131	Percentage of digestion (%)	Humeri n = 114	Ilia n = 125	Femora n = 120	Tibio-fibulae n = 131
Grade 0 (Complete)	82.5	72.8	94.2	82.4	Grade 0 - None	64.0	53.6	69.2	84.7
Grade 1	8.8	12.8	5.0	9.9	Grade 1 - Light	21.9	38.4	22.5	9.9
Grade 2	5.2	8.8	0.8	7.7	Grade 2 - Moderate	14.1	8.0	8.3	5.4
Grade 3	3.5	5.6	0	0	Grade 3 - Heavy	0	0	0	0
Total Breakage	17.5	27.2	5.8	17.6	Total Digestion	36.0	46.4	30.8	15.3

Neolithic cabin, while in ZB the cooked or consumed remains could have been redistributed.

Further evidence of human consumption is the presence of burning, which in Baume d'Ogens is seen on 59% of the bones, mainly affecting the ilia, which are burned in 73.27% of cases (Chiquet, 2005). The action of fire on anuran remains has been documented in Chalain 3, affecting 4.7% of the sample (Bailon, 1997), and 10.2% of the sample from pit 36 of Kutná Hora-Denemark (Kyselý, 2008). Also, the presence of cut marks on three bones (on a radio-ulna, tibio-fibula and coracoid) of *R. temporaria* from Arbon Bleiche has been identified as evidence of processing for human consumption (Hüster, 2004). Remarkably, this site also yielded remains of the endoparasitic nematode *Dioctophyma* in human faeces, an organism that uses anurans as transitory hosts during its lifecycle (Le Bailly and Bauchet, 2004). Further coprological evidence of the human consumption of frogs comes from level VI of Chalain 3, where human excrement was found to contain 59 remains of *R. temporaria*. Remains of this species were also found in seven dog coprolites. In all cases the anuran bones presented very high breakage and extreme digestion modifications (Bailon, 1997).

These characteristics associated with human consumption, mainly the preferential selection of anatomical parts and the evidence of thermal alterations by the action of fire or cut marks, have not been found in El Mirador. Moreover, the tree frog *Hyla* is very small and therefore provides very little meat compared to edible frogs, which in Europe belong to the Ranidae family (Mattison, 2011).

The accumulation of a large number of *P. punctatus* (MNI = 176) in level 1a from the latest Pleistocene of Bois-Roche cave (Charente, France) has been associated with a catastrophic mortality caused by flash floods in the cave during the period of hibernation or estivation of the anurans inside it (Cochard, 1998, 2004). The remains of *P. punctatus* were distributed in several small taphocenoses across the horizontal plane of the level, preserving all elements of the skeleton and, in general, had a comparatively high PR of 52.3% of the total. Breakage in the Bois-Roche sample affects 79.7% of the remains, but no evidence of digestion has been identified, so the high fracture percentage has been linked to a conservation factor during sedimentation or after it, without significant negative impact from other abiotic agents (Cochard, 2004).

The sex and age determinations in Bois-Roche point to a majority of females (> 65%) compared to males (< 15%), as well as to the existence of immature juveniles (< 20%). This suggests that the catastrophic mortality event took place at the beginning of spring, as immature individuals and males of *P. punctatus* abandon the winter shelters before the females (Cochard, 2004). This demographic sample from Bois-Roche contrasts with Chalain 3 and Kutná Hora-Denemark, which show very marked biases in favour of males: in level VI of Chalain 3 the male frogs represented 70% of the individuals (Bailon, 1997), while in pit 36 of Kutná Hora-Denemark the percentage of males climbs up to 94.12% (Kyselý, 2008). In Baume d'Ogens, of a total 96 MNI, only the presence of 18 MNI-male could be sexed compared to 10 MNI-female (Chiquet, 2005). Bailon (1997) and Kyselý (2008) link the high representation of males and adult individuals in the accumulations with a systematic (for Kyselý) or opportunistic (for Bailon) hunting strategy of *R. temporaria* for human consumption during its reproduction period, between February/March to April, when the males are concentrated in ponds waiting to attract the females with sonorous calls.

5.2. Coprocenotic scenario, a natural history

The recovery of very compact cylindrical or oval-shaped accumulations of microvertebrate remains and the presence of multiple taphonomic alterations associated with non-human animal predation, such as digestive corrosion effects, during the fieldwork at El Mirador are concordant with a coprocenotic origin. The thinning and collapse of the bone walls and the low degree of rounding at the edges of the fractures, together with the relatively low degree of gastric alterations, rules out any carnivorous mammal as their source and suggests an avian raptor as the accumulation producer (Pinto Llona and Andrews, 1999).

The absence or presence of anthropogenic marks cannot be used to directly determine the human or non-human origin of the accumulation. The anuran and squamate remains from El Harhoura 2 cave (Morocco) show the continuous presence of burning throughout its sequence, reaching up to 9% of the total elements in Level 1, dated to the Neolithic (5800 BP, Stoetzel et al., 2012). But the presence of burnt anuran bones in El Harhoura 2 is not related to a specific pattern of burning or cut marks but rather they appear at an ashen layer, so they have been interpreted as post-depositional effects and probably accidentally burnt (Stoetzel et al., 2011, 2012). In the Neolithic level 1, one radio-ulna of *Bufo* s.l. have been found with traces looking like anthropic cut marks (ten parallel but irregular striations), which have been identified as possible evidence of marginal human consumption of toads during the Neolithic period, although most of the characteristics associated with human consumption are missing (preferential selection of body parts, chewing marks, intentional burns, more flesh marks) (Stoetzel et al., 2012). A category 1–2 predator has been postulated as the main accumulator of anuran remains in El Harhoura 2, possibly a medium-sized owl such as *Bubo ascaphalus* (Stoetzel et al., 2012).

The PR in anurans from Level 1 of El Harhoura 2 shows a low representation of most elements in comparison with El Mirador accumulation, with the highest values in tibio-fibulae (100%), radio-ulnae (68.2%) and ilia (59.1%), and highlights the very low representation of femora (9.1%) (Stoetzel et al., 2012). The low total PR of this assemblage (27.4%) is possibly because it is material dispersed over an extensive archaeological level (25 m^2) (Stoetzel et al., 2008, 2010, 2011, 2012) (Fig. 8). The presence of 140 anuran individuals (117 *Discoglossus galganoi*, 20 *R. temporaria* and 3 *Hyla molleri*) was documented in a large contemporary accumulation generated by *T. alba* from Asturias, northern Spain (Rey and Sanchiz, 2005). The total PR is very high (78.9%), in accordance with that was assigned to *T. alba* (e.g., Andrews, 1990; Pinto Llona and Andrews, 1999), with the lowest value of the assemblage for the cranial bones (53.9%), and the highest values for the ilium (94.2%), the urostyle (91.2%), and the tibio-fibula (90.1%) (Rey and Sanchiz, 2005) (Fig. 8).

The literature on Iberian current populations document the predation of *Hyla* by the nocturnal owls *T. alba* and *Athene noctua*, and the diurnal kestrel *Falco tinnunculus* (Rey and Sanchiz, 2005; Diego-Rasilla and Ortiz-Santaliestra, 2009), but the digestion evidence and breakage in El Mirador accumulation and their percentages are not consistent with any of these species (Andrews, 1990; Pinto Llona and Andrews, 1999). If the criteria for amphibian taphonomy established by Pinto

Table 5
Characteristics of the main accumulations of anurans in archaeological contexts from Late Quaternary in Western Palearctic.

Site	El Mirador	El Harboura 2	Bois-Roche	Chalain 3	Kutná Hora-Denemark
Typology	Cave	Cave	Cave	Open air settlement	Open air settlement
Level	MIR5	1	1a	N.VI	F.36
Dimensions (taphocenosis)	Concentrated in a massive accumulation of 7.8x2.7 × 2.4 cm	Dispersed in 25 m^2, thickness 20–180 cm	Concentrated in 1 m^2, thickness 10–12 cm	Dispersed in 84 m^2, thickness 5 cm	Dispersed inside a pit of 1.4 × 1.2 × 0.25 m
Chronology	Chalcolithic	Neolithic	Late Pleistocene (MIS5-4)	Neolithic	Chalcolithic
Dominant species % (NMI)	*Hyla* gr. *arborea* (*Hyla molleri*) 84% (66 NMI)	*Bufo* s.l. (*Bufo spinosus* and *Sclerophrys mauritanica*) 64% (11 NMI)	*Pelodytes punctatus* 89% (174 NMI)	*Rana temporaria* 99% (868 NMI)	*Rana temporaria* 100% (123 NMI)
Breakage	Yes	Yes	Yes	Yes	Yes
Digestion	Yes	Yes	No	Yes	No
Burning	No	Yes	No	Yes	Yes
Cut marks	No	Yes	No	Yes	No
Other marks or evidences	Post-depositional alterations (root marks)	Post-depositional alterations (root marks, black traces, coating, burning, corrosion, rounding weathering, trampling)	Post-depositional alterations (fragmentation)	Human and dog coprolites	Post-depositional alterations (possible trampling)
Hypothesis	Owl predation, pellet	Owl predation, possible marginal human consumption	Catastrophic mortality	Human consumption, marginal canine consumption	Human consumption
References	This study	Stoetzel et al., 2008,2010, 2011, 2012	Cochard, 1998, 2004; Blain and Villa, 2006	Bailon, 1997	Kyselý, 2008

Llona and Andrews (1999) are used, the breakage category 2 documented in *H.* gr. *arborea* is coincident with the proposal for the tawny owl, *Strix aluco*, but this nocturnal raptor is ascribed to a higher digestion category (4). The available data for the digestion marks in anuran bones do not indicate any raptor with a digestion category 2, with category 1 being the closest value, which includes only the barn owl (*T. alba*), although its alterations to bones are practically null or very low (Pinto Llona and Andrews, 1999; Denys et al., 2018). On the other side, anuran remains associated with predation by carnivorous mammals show much higher degrees of digestion and breakage, categories 4–5 (e.g., Cobrante cave, Martín et al., 2009).

In analogous criteria established by Andrews (1990) for the digestion and breakage in the post-cranial skeleton of small mammals, breakage category 2 includes the spotted eagle-owl, *Bubo africanus*, and the eagle-owl, *Bubo bubo*, while digestion category 2 includes *S. aluco*, *B. africanus* and *B. bubo*. The possible assignment to *B. bubo* or *S. aluco*, based on the categorisations of Andrews (1990), would come into conflict with breakage category 3 and digestion category 5 proposed for *B. bubo* and breakage category 2 and digestion category 4 proposed for *S. aluco* in Pinto Llona and Andrews (1999). Though the rodent remains in the taphocenosis are very scarce for a better interpretation (25 MNE, 1.23%), in general, they show alterations compatible with a predator with a degree of light-intermediate modification, according to Andrews (1990), which is consistent with the anuran data. However, new data have shown the existence of seasonal variation between winter-summer in the degrees of digestion produced by *S. aluco*, specially in rodent molars and incisors (Andrews and Fernández-Jalvo, 2018). Other factors could have influenced the taphonomy and generated differences between the comparison samples, such as the age of the predator, the time of digestion, the variations in tissues between amphibians and rodents, the number of preys in the intake or the consumed biomass. These variables demand greater caution in the identification of the predator. The same applies to data on breakage, which should be considered with prudence, since they may be affected by post-depositional processes.

The eagle-owl is a generalist and opportunistic predator, which, on the Iberian Peninsula, hunts a wide range of herpetofauna species (*Bufo spinosus*, *Pelophylax perezi*, *Pelobates cultripes*, *Mauremys leprosa*, *Podarcis hispanica* sensu lato, *Psammodromus algirus*, *T. lepidus*, and Colubridae snakes) (Hiraldo et al., 1975; Pérez-Mellado, 1978; Vericad et al., 1976; Serrano, 1998; Penteriani and Delgado, 2016). Some individuals of *B. bubo* can specialise in certain prey groups, including anurans (Andrews, 1990). For example, in Hohe Tauern (Salzburg, Austria), frogs account for 48% of the MNI of the eagle-owl's diet while in Rogaland (Vestlandet, Norway) they represented 45.58% of the MNI. In both cases, they constitute the primary prey group (Hagen, 1950; Frey and Walter, 1986).

Although *S. aluco* is commonly considered a nocturnal species, much more than *B. bubo*, the record of lizards (*Lacerta schreiberi* and *Podarcis muralis*) in the diet of the tawny owl of León and Asturias indicates its predation on typically diurnal species (Nores, 1980; Alegre et al., 1989). Frogs represent 9.2% of the MNI in the diet of *S. aluco* of Scandinavia (Mikkola, 1995) and amphibians up to 10.40% in Poland (Romanowsky and Żmihorski, 2009). A similar percentage was obtained in a German macro-study of > 72,000 preys of tawny owls, in which the anurans accounted for 10.2% of the MNI (Uttendörfer, 1952). Due to the large size of the accumulation (7.8x2.7x2.4 cm), it corresponds more accurately to a *B. bubo* pellet than to a *S. aluco* pellet (Mikkola, 1995), unless it was a very large tawny owl.

Regardless of the predator that generated the accumulation, the inclusion in the taphocenosis of at least 66 adult individuals of tree frogs suggests that it was formed during a period with an abundance of tree frogs in the environment. Currently, the Iberian Peninsula is inhabited by two species of tree frogs, the Mediterranean tree frog, *Hyla meridionalis*, which arrived recently from the Maghreb (Recuero et al., 2007), and the endemic Iberian tree frog, *H. molleri*, which belongs to

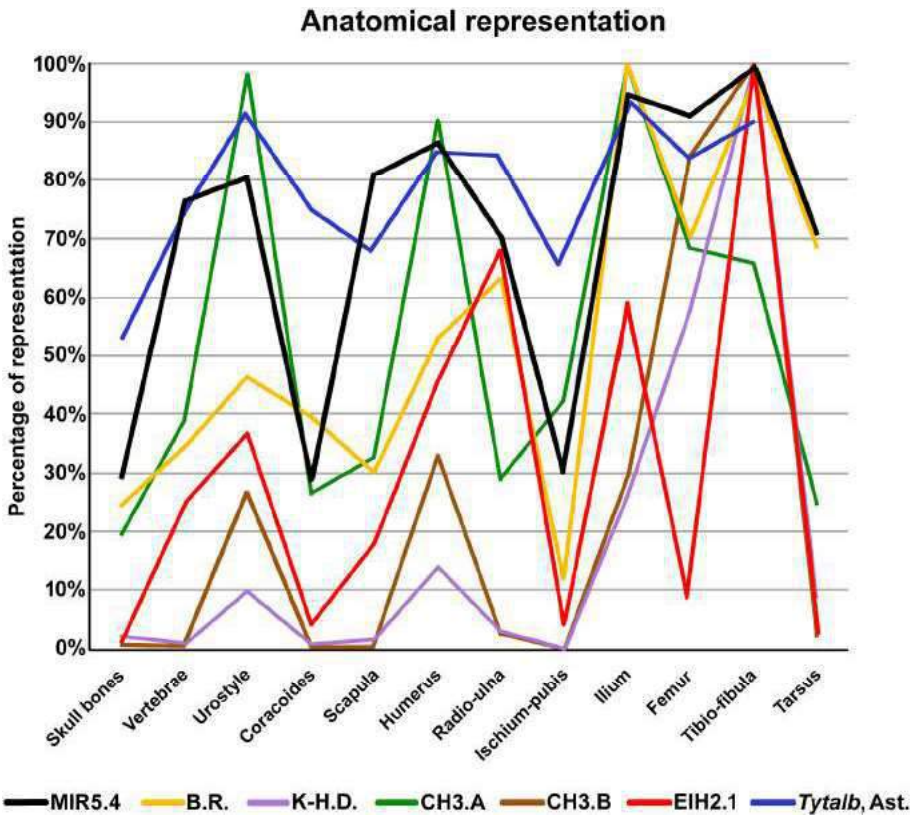

Fig. 8. Comparison between the percentages of representation (PR) of each bone element in *Hyla* gr. *arborea* (*Hyla molleri*) of the taphocenosis MIR5-P21-n4 from El Mirador cave (MIR5.4) compared with those obtained in *Pelodytes punctatus* from Bois-Roche (B.R., Cochard, 1998), in *Rana temporaria* from Chalain 3 n.VI ZA. and Chalain 3 n.VI ZB (CH3.A and CH3.B., Bailon, 1997), in *Rana temporaria* from Kutná Hora-Denemark F.36 (K-H.-D., Kyselý, 2008), in the anuran accumulation from Level 1 of El Harhoura 2 (ElH2.1, Stoetzel et al., 2012) and from modern *Tyto alba* accumulation from Asturias, Spain (*Tytalb*, Ast., Rey and Sanchiz, 2005).

the European *Hyla* gr. *arborea* taxon (Stöck et al., 2012). The most plausible option, for these biogeographical reasons, is that the tree frogs of El Mirador cave can be attributed to the native *H. molleri*.

In this species, the main concentrations of adults occur during the breeding season, when they gather in ponds with abundant vegetation between April and May (Lizana et al., 1989; Diego-Rasilla and Ortiz-Santaliestra, 2009). The reproduction begins with the arrival of males in groups of up to 20 per metre of shore. The males remain an average of 5.2 nights at the ponds, while 82% of females stay only one night (Márquez and Tejedo, 1990). The representation by sex in reproductive concentrations is skewed in favour of males, with biases ranging from 5.4:1 to 26.2:1 (García et al., 1987; Salvador and Carrascal, 1990).

The predation of an owl on *H. molleri* reproductive agglomerations could be the initial coprocenotic origin of El Mirador's taphocenosis. The avian raptor, which would use the cave as a nest or perch, opportunistically hunted an abundant seasonal resource in the environment, linked to the wet weather of spring. The multiple choruses of the males, whose calls are audible more than a kilometre away (Stumpel, 1997), made them easy prey at night, particularly if the hunted individuals were united in mating axillary amplexus, in the which the male holds the female by the armpits for hours or days (García-París, 2004). This may explain the ratio of 1.36:1 in favour of the males identified in El Mirador, which is very low in comparison with the minimum ratio (5.4:1) documented currently (García et al., 1987). After digestion, the owl regurgitated the pellet inside El Mirador cave, at that time used as a burial site during the Chalcolithic (Vergès et al., 2016), which would have allowed it to be included within the sedimentary record without being destroyed or disintegrated by other human activities.

6. Conclusions

The almost monospecific accumulations of anurans, mainly frogs (*R. temporaria*), from European archaeological sites have often been cited as linked to human consumption (Bailon, 1997; Hüster, 2004; Chiquet, 2005; Kyselý, 2008). These are taphocenosis that appear in prehistoric settlements as a product of the exploitation of meat from *R. temporaria*, often with evidence of processing and cooking. The exception comes from the Late Pleistocene of Bois-Roche (France), where an accumulation of *P. punctatus* is associated with a natural catastrophic mortality (Cochard, 1998, 2004). The case of the *Hyla* gr. *arborea* (*molleri*) taphocenosis MIR5-P21-n4 from El Mirador cave points to a different phenomenon. It was generated by the predation of a bird of prey (possibly a large tawny owl or eagle-owl) that opportunistically hunted an abundant seasonal resource. Both humans and avian raptors, despite the differences, hunt anurans during the breeding period, in which they are massively concentrated in bodies of water. These findings indicate the great importance that such small prey had in the subsistence diets in the past, and how the life cycles of small animals were exploited. The exceptional stratigraphy of El Mirador cave, which has provided more coprocenotic taphocenosis of microfauna with the abundant presence of herpetofauna, will serve to determine the importance of amphibians and reptiles in the animal trophic chains of the Holocene. Finally, it is necessary to highlight the importance and the need to study amphibian taphonomy in greater depth, including modern samples. Amphibian evidence is scarce and largely overlooked despite being, as this paper proves, essential in understanding the origin of the accumulations and their role in humans and non-human predators' diets in the past.

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Trade and stowaways: molecular evidence for human-mediated translocation of eastern skinks into the western Mediterranean

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Abstract. Human movements in the regions surrounding the Mediterranean Sea have caused a great impact in the composition of terrestrial fauna due to the introductions of several allochthonous species, intentionally or not. Reptiles are one of the groups where this anthropic impact is most evident, owing to the extensive intra-Mediterranean dispersals of recent chronologies. *Chalcides ocellatus* is a widespread skink with a natural distribution that covers almost the entire Mediterranean Basin. Two hypotheses have been proposed to explain its origin: natural dispersions and human translocations. Previous molecular data suggest the occurrence of a recent dispersal phenomenon across the Mediterranean Sea. In this study we present the first record of this species in the Iberian Peninsula, in Serra del Molar (South-east Spain). We combined molecular analyses and archaeological records to study the origin of this population. The molecular results indicate that the population is phylogenetically closely related to specimens from north-eastern Egypt and southern Red Sea. We suggest that the species arrived at the Iberian Peninsula most likely through human-mediated dispersal by using the trade routes. Between the Iron to Middle Ages, even now, the region surrounding Serra del Molar has been the destination of human groups and commercial goods of Egyptian origins, in which *Chalcides ocellatus* could have arrived as stowaways. The regional geomorphological evolution would have restricted its expansion out of Serra del Molar. These findings provide new data about the impact of human movements on faunal introductions and present new information relating to mechanisms of long-distance translocations.

Keywords: *Chalcides ocellatus*, DNA, introduction, Mediterranean Sea, reptiles, Spain, species dispersal.

Introduction

The Mediterranean Basin has been and still is a fascinating biogeographical framework presenting constant faunal exchanges, which have affected many of the faunas present on every shore of the Mediterranean and which have been augmented by human intervention (Pooley and Queiroz, 2018). The distribution and inferred phylogeographic patterns of reptiles such as the circum-Mediterranean geckos *Tarentola mauritanica* and *Hemidactylus turcicus* have suggested the existence of possible human interventions in their intra-Mediterranean dispersals (Harris et al., 2004; Carranza and Arnold, 2006; Rato et al., 2011, 2016; Stöck et al., 2016). This phenomenon has also affected the Iberian Peninsula, which shares many species,

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both reptiles and amphibians, with North Africa (Pleguezuelos et al., 2008). Human translocations with North African origin are proposed for the Iberian populations of the chameleon *Chamaeleo chamaeleon* (Paulo et al., 2002) and the treefrog *Hyla meridionalis* (Recuero et al., 2007). Other dispersals, on the other hand, have their origins in the Iberian Peninsula, for example, the translocation of the lizard *Podarcis vaucheri* in Greece (Spilani et al., 2018). In the Western Mediterranean context, the human-mediated introductions of herpetofauna in the Balearic Islands stand out, where the successive arrivals of different human groups led to the extirpation of native species in most of the main islands (*Alytes muletensis* and *Podarcis lilfordi*), besides the introduction of new species from other Mediterranean regions (e.g. *Bufotes balearicus*, *Emys orbicularis*, *Testudo hermanni*, *Podarcis sicula*, and *Hemorrhois hippocrepis*), from the Neolithic-Bronze Ages to the present (Pinya and Carretero, 2011; Valenzuela et al., 2016; Silva-Rocha et al., 2018).

Another reptile species with a practically circum-Mediterranean distribution is the ocellated skink, *Chalcides ocellatus*, which can be considered a species complex, with several deep lineages across North Africa (Carranza et al., 2008). This skink is widely distributed in the southern, central and eastern regions of the Mediterranean basin (fig. 1), from the eastern Moroccan coast to Anatolia, as well as on various islands in the Aegean Sea, Euboea, Crete, Cyprus, Tunisian Tabarka, Malta, Sicily, Conigli, Lampedusa, Lampione, Linosa and Sardinia, with continental European populations in and into the Attica peninsula (Kornilios et al., 2010). The species' distribution range also extends to the Near East, Mesopotamia, and the shores of the Red Sea, as far south as Somalia and Yemen, and in the Persian Sea region as far east as Pakistan (Anderson, 1999; Lavin and Papenfuss, 2012). There are currently introduced populations in Naples, Stromboli, Kasos and Sri Lanka (Caputo et al., 1997; Karunarathna et al., 2009; Lo Cascio and Grita, 2016; Kornilios and Thanou, 2016), as well as in Florida and Arizona (Krysko et al., 2011; Gunn et al., 2012). Three Algerian individuals were released in Marseille (France) and created a new population during the first decades of the 20th century, and an isolated individual was found in the railway goods yards of Cardiff (Wales) in 1944 (Siépi, 1913; Fitter, 1959; Kraus, 2009).

The large transcontinental distribution of *C. ocellatus*, together with the low molecular divergence and the hard polytomies observed among many of the populations assigned to the

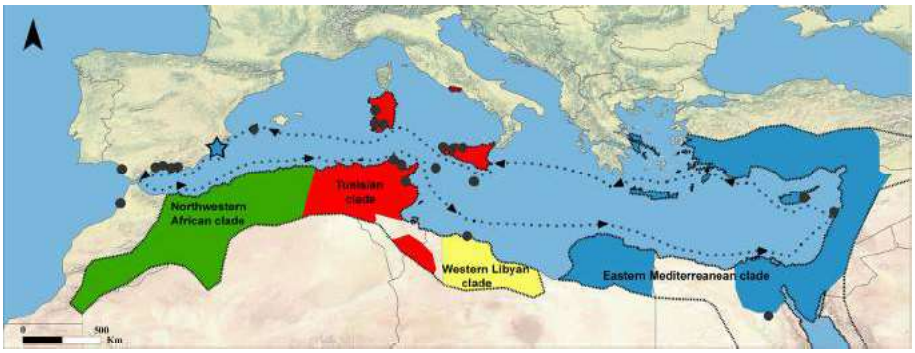


Figure 1. Mediterranean distribution range of *Chalcides ocellatus* according to its phylogenetic clades (Kornilios et al., 2010) and the geographic location of the Serra del Molar population (SE Iberian Peninsula; blue star). Arrows indicate the Phoenician intra-Mediterranean maritime routes and the main trade ports during the first Iron Age period (black dots) (based on Aubet, 2009).

eastern subclades, have made it possible to postulate the human-mediated introduction in recent times as a possible mechanism for its expansion (Kornilios et al., 2010; Lavin and Papenfuss, 2012), and even link it, at least in the context of the Mediterranean Sea, to the trade during the Ancient Age (Kornilios et al., 2010).

In this study, we report for the first time the presence of a reproductive population of the ocellated skink, *C. ocellatus*, in Serra del Molar (fig. 2). The geographic location of the population is a small coastal mountainous area in the southeast of the Iberian Peninsula, localised between the Mediterranean Sea and marsh areas originated by the Vinalopó and Segura rivers, in the southern Valencian Country. These individuals were morphologically identified as *C. ocellatus* (body elongate and cylindrical, tail almost equal to body length, ear without lobules, tympanum exposed, multiple dorsal *ocelli*; Baha El Din, 2006). Given that this is a species without current herpetological or archaeo-paleontological records in the Iberian Peninsula, molecular analyses were performed to confirm its identification and to determine the biogeographical origin of this newly discovered population.

Material and methods

Individuals of *C. ocellatus* were identified for the first time in April 2017 in Serra del Molar (38.1439N, −0.6569W, WGS; fig. 1). This area is part of the Elx municipality, in the Baix Vinalopó comarca within the Valencian province of Alacant/Alicante, in the grid UTM 30SYH02. The area where the discovery took place is between 35 and 75 meters above sea level, presents a Mediterranean thermos-type and is biogeographically located in the Alicantino subsector of the Murciano-Almeriense sector (Rivas-Martínez, 1987). It is a predominantly sedimentary area, formed at its base by calcareous sandstones of coastal marine origin on which outcrop conglomerates of silt, marl and fluvio-lacustrine sands (Almela et al., 1978). The area presents the typical thermo-Mediterranean scrub communities (*Brachypodium retusum*, *Macrochloa tenacissima*, *Rosmarinus officinalis*, *Chamaerops humilis*) with concentrations of *Pinus halepensis*, and only the lower parts show evidence of abandoned plots for cultivation of olives (*Olea europaea*) and carobs (*Ceratonia siliqua*), although today most of them are covered by xerophilous and heliophilous scrubs. The archaeological remains of the Iberian settlements of La Escuera and El

Figure 2. Individuals of *Chalcides ocellatus* from Serra del Molar (SE Iberian Peninsula): (A) Adult male (♂ n.3, CN12645); (B) Adult male (♂ n.4); (C) Gravid female (♀ n.2); (D) Adult male in its habitat (♂ n.5, CN13391).

Table 1. Morphometric data of the *Chalcides ocellatus* individuals from Serra del Molar. Specimens used for the genetic identification are with their corresponding code. (*) = autotomized and partially regenerated tails.

Individuals	Body length (SVL; in mm)	Tail length (in mm)	Total length (in mm)	Tail/body ratio
Male n.1 (01.04.2017)	95.2	100.5	195.7	1.05
Male n.2 (01.04.2017)	85.8	91.9	177.7	1.07
Male n.3, CN12645 (07.10.2017)	99.1	101.7	200.8	1.02
Male n.4 (20.04.2018)	102.1	76.8*	178.9	0.75
Male n.5, CN13391 (18.05.2018)	97.2	73.2*	170.4	0.75
Female n.1 (02.04.2017)	96.0	92.4	188.4	0.96
Female n.2, gravid (11.06.2017)	105.1	115.4	220.5	1.09
Female n.3, gravid (11.06.2017)	89.4	90.7	180.1	1.01
Female n.4, CN12564 (08.10.2017)	84.3	86.6	170.9	1.03
Female n.5 (20.04.2018)	84.3	35.4*	119.7	0.42
Female n.6, CN13435 (18.05.2018)	78.4	89.3	167.7	1.14
Female n.7, CN13434 (18.05.2018)	76.8	83.5	160.3	1.08
Median $\pm$ Standard error (SE)	91.14 $\pm$ 2.738	86.45 $\pm$ 5.658	177.59 $\pm$ 7.115	0.95 $\pm$ 0.142
Median $\pm$ Standard error (SE) (without autotomized tails)	90.01 $\pm$ 3.265	94.67 $\pm$ 3.259	184.68 $\pm$ 6.252	1.05 $\pm$ 0.111

Oral, and the necropolis of El Molar are located in the surroundings (Grau and Moratalla, 2001). According to data from official herpetological agencies (AHE, 2018; BDB-GVA, 2018), the reptiles of this area had not been surveyed previously by any herpetologist or scientific group.

In collaboration with the Valencian environmental authorities, successive surveys were carried out in this locality to monitor their presence in the area, to obtain data on their spatial distribution and morphology, and to obtain tissue samples for genetic analyses. Twelve identified individuals were captured to obtain morphometric data and subsequently released (table 1). Each individual has been sexed by pressing gently around the cloacal region to find the hemipenises, if males. Importantly, this process was conducted avoiding the total eversion of hemipenises to avoid potential injuries for the animals.

Genetic sampling, DNA extraction and amplification

In order to perform molecular analyses, tissue samples were taken from five individuals with the following sample codes: CN12564 and CN12645 were collected during October 2017, and CN13391, CN13434 and CN13435 were collected in May 2018. To understand the geographic origin of these newly discovered Valencian individuals, sequences of other *C. ocellatus* specimens from distinct localities around the Mediterranean Basin and across the species' distribution range, were retrieved from GenBank. Two specimens of *Chalcides montanus* have been included as outgroup (Carranza et al., 2008; Kornilios et al., 2010) (see supplementary table S1 and supplementary fig. S1).

Genomic DNA was extracted from alcohol-preserved tissue samples using the SpeedTools Tissue DNA Extraction kit (Biotools, Madrid). A fragment of 303 bp of the mitochondrial gene Cytochrome b (*cytb*) was amplified by the Polymerase Chain Reaction (PCR). The following primers for amplification and sequencing were modified from Kocher et al. (1989): Cytb1 (5′-CCATCCAACATCTCAGC ATGATGAAA-3′) and Cytb2 (5′-CCCTCAGAATGATATT TGTCCTCA-3′). We performed PCR in a volume of 25 μl with an initial denaturation step of 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 80 s, annealing at 50°C for 45 s, and extension at 72°C for 1 min; final extension step was set for 72°C for 5 min. Amplicons were visualized on a 1% agarose gel stained with SYBR Safe DNA gel stain (Invitrogen Corp., Carlsbad, CA, USA). Purification and bi-directional sequencing were carried out by Macrogen (Macrogen Inc.). Chromatographs were checked and the forward and reverse sequence contigs for each sample were assembled and edited using Geneious v.7.1.9 (Biomatter Ltd.). Sequences were aligned using MAFFT v.7.3 (Katoh and Standley, 2013) with default parameters. We translated

the final alignment into amino acids and no stop codons were detected.

Phylogenetic analyses

Phylogenetic analyses were performed under maximum likelihood (ML) and Bayesian inference (BI) frameworks. The ML analysis was conducted in RAxML v.8.1.2 as implemented in raxmlGUI v.1.5 (Silvestro and Michalak, 2012). The analysis was performed with the GTR+G model of sequence evolution and 100 random addition replicates. Nodal support was assessed with 1000 bootstrap replicates. The BI analysis was conducted with BEAST v.1.8.4 (Drummond et al., 2012). We used jModelTest v.2.1.7 (Guindon and Gascuel, 2003; Darriba et al., 2012) to select the best model of nucleotide substitution under the Bayesian information criterion (BIC). We carried out the BEAST analysis with the following priors (otherwise by default): TrN+G model; Coalescent: Constant size tree model; random starting tree; alpha prior uniform (0–10); uncorrelated relaxed clock (uniform distribution; 0–1). Three individual runs of 2×10^6 generations were carried out, with sampling at intervals of 2×10^3 generations. Convergence, posterior trace plots, effective sample sizes (>200), and burn-in were evaluated with Tracer v.1.6 (Rambaut et al., 2014). The tree runs were combined in LogCombiner discarding the first 10% of the trees as burn-in and the ultrametric tree was generated with TreeAnnotator (both available in the BEAST package). Phylogenetic trees were visualized with FigTree v.1.4.3 (Rambaut and Drummond, 2010).

Results

Between April 2017 and May 2018, 35 individuals of *C. ocellatus* were identified, from which morphometric measurements of 12 distinct individuals could be obtained, all were adults (snout-vent length, SVL > 55 mm, Çiçek et al., 2013) (table 1). The different attested stages of ontogenetic development have allowed verifying the existence of a breeding population, with young and adult individuals, besides the presence of gravid females (fig. 2c). The population is distributed at least in a spatial range of 5.2 km^2.

The preliminary taxonomic assignment of Serra del Molar individuals into *C. ocellatus* has been confirmed, following the criteria of Baha El Din (2006) and Carranza et al. (2008): primitive corporal form within the *Chalcides* genus, elongate and cylindrical; black and white dorsal *ocelli*; atrial overture markedly visible, with exposed tympanum; biometric tail/body ratio (tail length divided by distance from snout tip to cloaca) very close to value 1 (average: 1.05, range: 1.14–0.96; table 1); pentadactyl front limbs with phalangeal formula 2.3.4.4.3; and pentadactyl hind limbs with phalangeal formula 2.3.4.5.3. The animals present the typical body-form and colouration pattern of the subspecies *C.ocellatus ocellatus* (fig. 2).

Phylogenetic structure

The dataset of the *cytb* gene used in the phylogenetic analyses included 153 sequences of *C. ocellatus* and had a total length of 303 bp: five newly discovered individuals from Spain, 146 sequences from across the Mediterranean Sea and adjacent regions, and two specimens of *C. montanus* (see supplementary table S1 and fig. S1). The ML and BI phylogenetic trees present a structure of three clades within *C. ocellatus* (fig. 3, supplementary fig. S1) separated into the eastern, central and western coastal areas of the Mediterranean Sea. Within these clades, a geographic grouping of specimens is apparent, although with an unsupported topology. In both the ML and BI analyses, Serra del Molar individuals are nested within a clade with specimens from the eastern Mediterranean region.

Four of the five Spanish specimens (CN12645, CN13391, CN13434 and CN13435) cluster together with two Egyptian individuals with high support (bootstrap and posterior probability values, 96 and 1, respectively). These Egyptian specimens (co50-FJ980237 and co51-FJ980238; Kornilios et al., 2010) were collected from Ras El Barr, in the Damietta Branch of the eastern Nile Delta. The sequences of these six specimens (Serra del Molar-Spain and Ras El Barr-Egypt) are almost identical, apart from one single mutation in position 159 where the Spanish specimens have an A, whereas the Egyptian specimens have a G. The fifth Spanish individual (CN12564) has a different phylogenetic position, clustering with samples from Egypt (including four

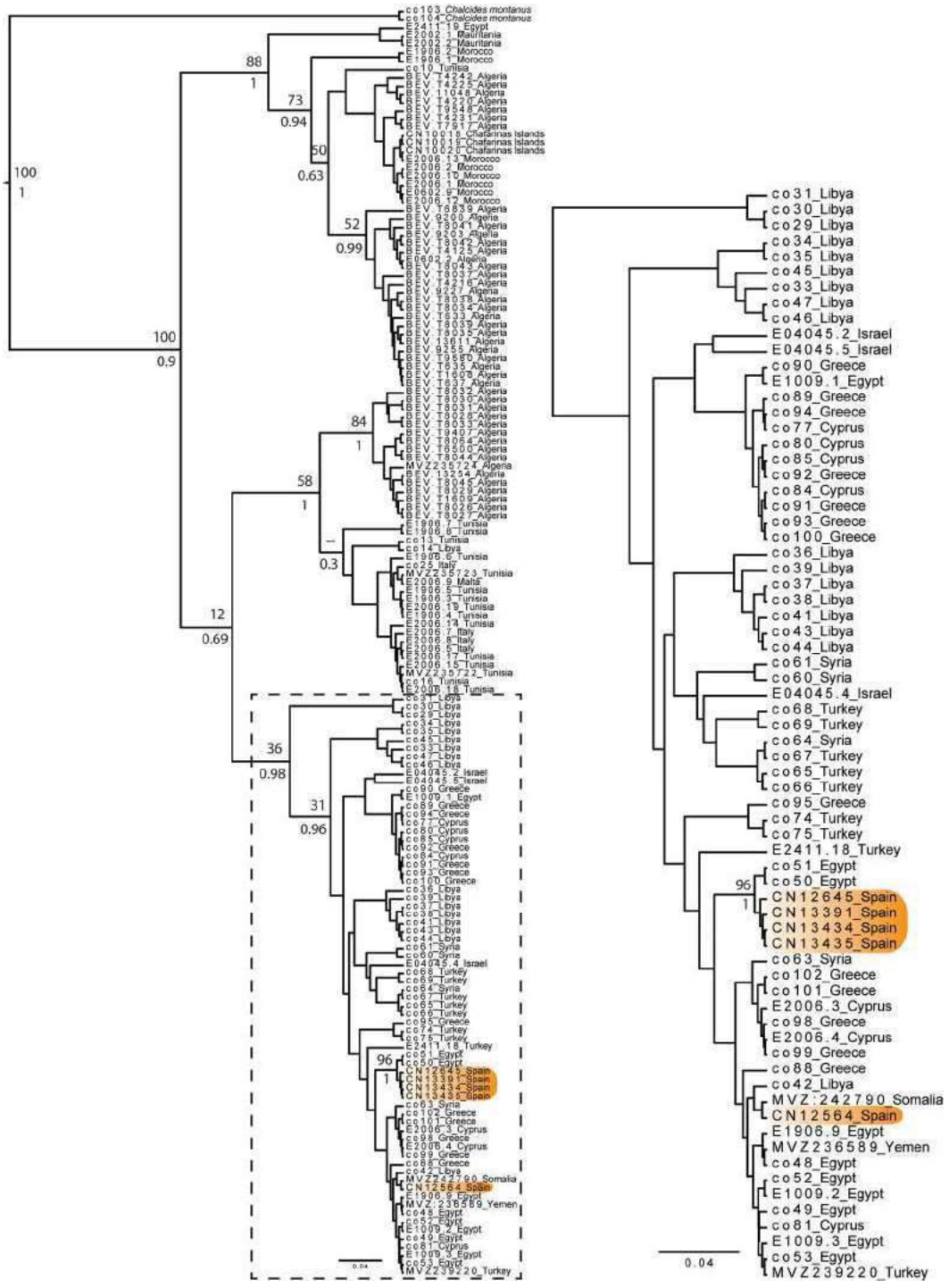


Figure 3. Bayesian Inference Cytochrome *b* phylogenetic tree of *Chalcides ocellatus*. Bootstrap (ML) and Bayesian posterior probabilities (BI) support values are indicated above and below the nodes, respectively. The newly discovered Spanish specimens collected from Serra del Molar are highlighted. Sample codes and localities correlate to specimens in supplementary table S1.

Egyptian specimens that were collected from Ras El Barr, co48-FJ980235, co49-FJ980236, co52-FJ980239 and co53-FJ980240), Somalia, Libya, Yemen, Turkey, Syria, Greece, and Cyprus, although with no support. This specimen's sequence is different from the other Spanish individuals in seven positions (in sites: 60, G *vs.* A; 96, A *vs.* C; 105, T *vs.* C; 129, C *vs.* G; 144, T *vs.* C; 204, G *vs.* A; 285, C *vs.* T, respectively).

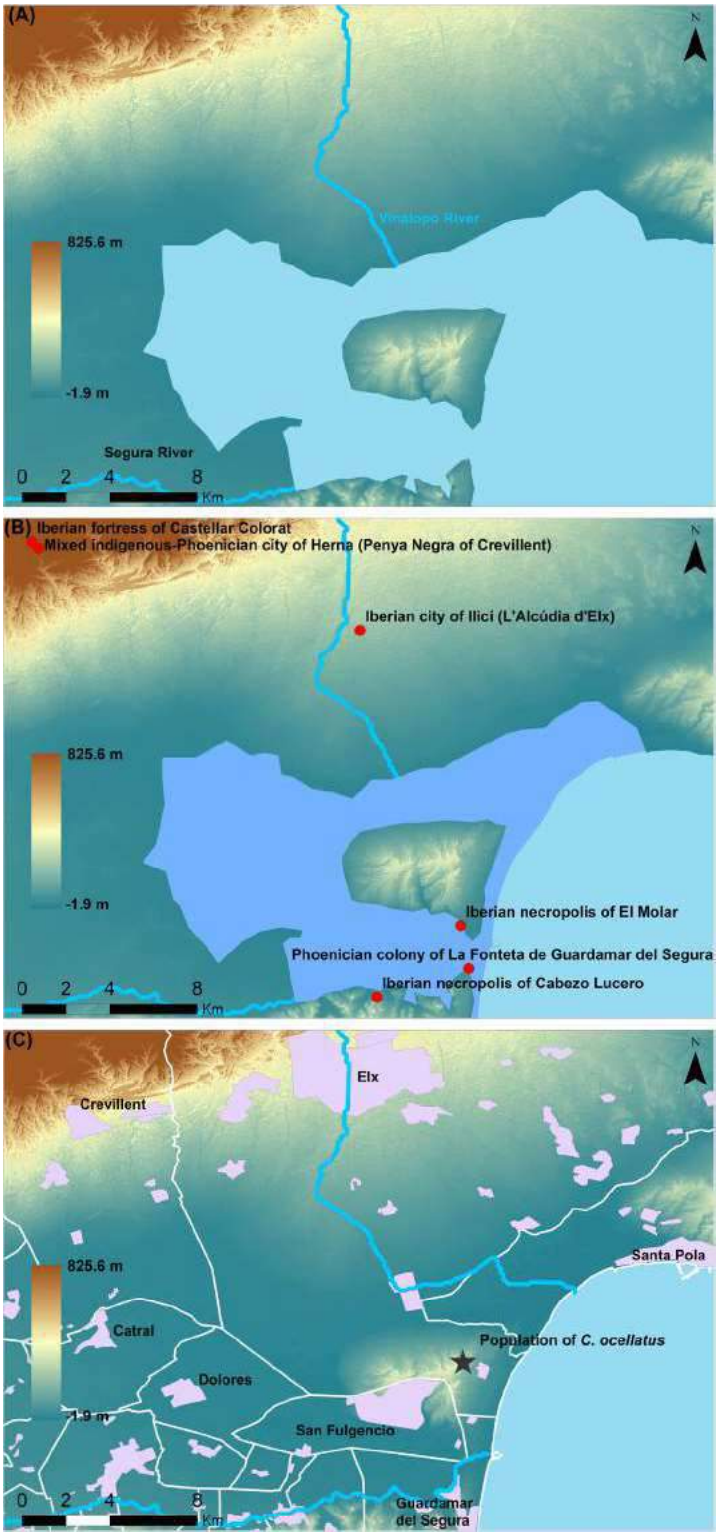
Discussion

Two hypotheses have been proposed to explain the origin of the Mediterranean populations of *C. ocellatus*: natural dispersal (maritime, continental or through temporary terrestrial bridges) and human translocations (Lavin and Papenfuss, 2012). The molecular results rule out any scenario of natural colonization of *C. ocellatus* in Serra del Molar: the phylogenetic tree assigned Serra del Molar individuals within subclade A2, distributed across the eastern Mediterranean basin (Kornilios et al., 2010) and exclude their arrival by "rafting" or other natural dispersal by sea from the Tunisian, Algerian or Moroccan coasts, which are the nearest natural populations of ocellated skinks (Martín et al., 2017; Beddek et al., 2018). Additionally, the populations of *C. ocellatus* from these Maghrebian countries belong to other phylogenetic clades (Carranza et al., 2008; Kornilios et al., 2010; fig. 3, supplementary fig. S1). Moreover, the extremely low genetic divergence found in the molecular data and the phylogenetic position of the Serra del Molar individuals allow to rule out their spread by land through a continental bridge within a very old paleogeographic scenario (for example, during the Messinian Salinity Crisis). Therefore, the genetic assignation in the eastern Mediterranean subclade implies that the only reasonable and plausible scenario is the human-mediated translocation.

The presence of a genetic admixture among the ocellated skinks from Serra del Molar (supplementary table S1 and supplementary fig. S1), which has been identified in other human-mediated lizard introductions (Kolbe et al., 2007; Santos et al., 2019), suggests the concurrence of at least two translocation events with distinct sources that originated the new population, or a single introduction with individuals from multiples origins, or that the admixture was already present at the original population or locality, as happens in Ras El Barr.

The dispersal mechanism linked to human activities has been one of the explanations given to the wide distribution of *C. ocellatus* (Schneider, 1981; Anderson, 1999) and is consistent with the phylogenetic studies (Carranza et al., 2008, Kornilios et al., 2010; Lavin and Papenfuss, 2012). In fact, there is a historical record of its introduction into Naples in a shipment of orange trees from Sicily during the 18th century AD (Caputo et al., 1997). Other authors propose different translocation methods, like the use of sand ballasts and their subsequent abandonment in port areas of the Persian Sea (Anderson, 1999). The widespread distribution of the subclade A2 in Kornilios et al. (2010) has been associated with maritime exportation routes of the *Silphium* plant during the Ancient Age (7th-2nd centuries BC), a trade originating in Libyan-Hellenic Cyrenaica (Amigues, 2004), as one of the ways by which *C. ocellatus* expanded through the Eastern Mediterranean (Kornilios et al., 2010).

The regional archaeological record of Serra del Molar has many peculiarities that allow us to postulate the possibility of an introduction due to intra-Mediterranean maritime trade. The surrounding region presents an important archaeological record linked to trade with the Eastern Mediterranean and Phoenician colonization during the second quarter of the 1st millennium BC, associated with the Phoenician colony of La Fonteta (Guardamar del Segura), which is located 2.5 kilometres from Serra del Molar (González, 2010a, b; Doménech, 2010) (fig. 4b).


(A)
N
Vinalopo River
825.6 m
-1.9 m
Segura River
0 2 4 8
Km
(B) Iberian fortress of Castellar Colorat
Mixed indigenous-Phoenician city of Herna (Penya Negra of Crevillent)
Iberian city of Ilici (L'Alcúdia d'Elx)
825.6 m
-1.9 m
Iberian necropolis of El Molar
Phoenician colony of La Fonteta de Guardamar del Segura
Iberian necropolis of Cabezo Lucero
0 2 4 8
Km
(C)
N
Elx
Crevillent
825.6 m
Santa Pola
Catral
Population of C. ocellatus
Dolores
-1.9 m
San Fulgencio
0 2 4 8
Km
Guardamar del Segura

The five sequenced individuals from Serra del Molar belong to the same subclade A2 in Kornilios et al. (2010) and appear to be mainly linked with the Egyptian specimens sampled from Ras El Barr, in the Nile Delta. During the ancient past, in this same area of Lower Egypt were seaports that traded with other regions across the Mediterranean Sea, such as Naukratis, Thonis-Heracleion, Tamiat, Pelusium and Tell el-Ghaba (Stanley et al., 2008; Pfeiffer, 2010; Lupo and Kohen, 2010), all of them were active harbours during the same period as La Fonteta colony (8th–6th centuries BC). In this Phoenician settlement and in nearby contemporary sites, a large amount of Egyptian objects has been discovered together with other manufactures from eastern workshops (Padró, 1975; Doménech, 2010; Escolano, 2012; López and Velázquez, 2012; González, 2014; Martínez and Vilaplana, 2014).

A possible route for the ocellated skink translocation is its arrival as an unintentional cargo passenger along with merchandises from Egypt (or another nearby eastern Mediterranean region) to the Phoenician colony of La Fonteta and its later establishment in the periphery of one of its associated Iberian settlements located in Serra del Molar, which was part of its most direct area of influence. The skinks could have arrived inside imported plants or soils, as is proposed by Kornilios et al. (2010) as way for human-mediated dispersals of *C. ocellatus* in the eastern Mediterranean regions, in which the skinks were transported as involuntary stowaways. For example, another agricultural product that could be the transport means for the translocation were eastern varieties of vine strains (*Vitis vinifera*), during the introduction of viticulture in Iberia by the Phoenicians themselves (Buxó, 2008; Iriarte et al., 2016). The molecular data of the conifer *Tetraclinis articulata* from the nearby Sierra de Cartagena (Murcia), which suggest the introduction or local genetic substitution through translocations from Tunisia by the Phoenicians/Carthaginians (Sánchez-Gómez et al., 2013), show the human-mediated mobility of plant species across the Mediterranean Sea during this same chronology.

In the context of ancient Mediterranean interactions, similar mechanisms of translocation have been proposed for the colonization of *Vipera aspis hugyi* on the island of Montecristo (Masseti and Zuffi, 2011) and the introduction of *Eryx jaculus* in the Licata region, Sicily (Insacco et al., 2015). The presence of ocellated skinks in this Iberian region, archaeologically linked to the Eastern Mediterranean, reinforces the hypothesis of Kornilios et al. (2010) about the ancient trade as the main phenomenon for the dispersal of *C. ocellatus*, and reinforces Egypt as the possible main point of the human-mediated translocations.

However, the links between the Iberian southeast with the Eastern Mediterranean, and especially with Egypt, are not limited to the phenomena of Iron Age trade and Phoenician colonization, because the intra-Mediterranean contacts continued during the Roman dominion. More recent historical relations with Egypt occurred during early Middle Age, when Islamic Egyptian troops colonized the surrounding region of *Tudmîr* in 743 AD (Gutiérrez, 1996; Vallvé, 1999). The Middle Age manuscripts also relay the existence of direct trade between *Tudmîr* and the harbours of the Fatimite Caliphate and Ayyubid Sultanate, particularly the Egyptian port of Alexandria (Azuar, 2016).

Figure 4. Biogeographical scenario for a Phoenician translocation of *Chalcides ocellatus* into the south-eastern Iberian Peninsula. (A) Serra del Molar as an island, isolated from the mainland by the Mediterranean Sea, during most of the Holocene. (B) Reconstruction of the area during the 8th-6th centuries BC, the formation of a coastal lagoon environment, the position of La Fonteta Phoenician colony and the main findings of objects with Egyptian origin (red point) in the southern Valencian Country. (C) Current situation of Serra del Molar and the current locality of the *Chalcides ocellatus* population (star). *Paleoenvironmental reconstruction of Serra del Molar during the Holocene to the present is based on Blázquez (2001), Grau and Moratalla (2001), Blázquez and Usera (2010), and Tent-Manclús (2012).

One of the most important contributions that the Muslim period had in the southern Valencian area was the introduction of the "oasis crop". Its greatest exponent is the "*Hort de Palmeres d'Elx*" (Palm Grove of Elche), a large monoculture concentration of the date palm (*Phoenix dactylifera*) originated in the 10th century AD that continues at present (Azuar, 1998). During the last decades, palm trees have additionally been used as ornament in private gardens and public parks. This requirement for new trees, which could not be serviced only by local production, was supplied by importing plants from Argentina and Egypt (Berbegal, 2017). Due to the growing demand, the invasive red palm weevil (*Rhynchophorus ferrugineus*) was introduced in Spain mainland through the entry of Egyptian palms without phytosanitary control in 1995 (Ferry and Gómez, 2002). The importation of Egyptian palm trees or another anthropogenic factors (including the current pet trade) may also explain a more recent origin for the translocation and colonization of Serra del Molar. In addition, *C. ocellatus* have demonstrated a high capacity to colonize new areas due to passive dispersals, recently documented in the islands of Stromboli (Italy) and Kasos (Greece) or even in America mainland (Florida and Arizona), where the ocellated skink was absent in thorough herpetological surveys a few years ago (Krysko et al., 2011; Gunn et al., 2012; Lo Cascio and Grita, 2016; Kornilios and Thanou, 2016).

Regardless of the possibility of an introduction during Phoenician times, Islamic period or more recently, the evolution of the Serra del Molar's environment could explain the survival of an allochthonous population. Although currently it is connected to the continent (fig. 4c), in the recent past Serra del Molar was an isolated island in front of the deltas of the Vinalopó and Segura rivers (fig. 4a). Recently, the sediments by both rivers settled and filled the area, encircling Serra del Molar to the west and north sides to form a lagoon environment of marshes, swamps and flood plains, which remained with brackish marsh conditions until the 18th century AD (Blázquez, 2001; Grau and Moratalla, 2001; Blázquez and Usera, 2010; Tent-Manclús, 2012) (fig. 4b).

The preservation of quasi insular conditions until relatively recent times (fig. 4c) could have enabled the survival of *C. ocellatus*, in case of an ancient introduction. To date, we were only able to locate individuals of ocellated skink in the north-east quadrant of Serra del Molar, which comparatively has suffered less anthropic impact, although this range may be much larger due to the fossorial cryptic nature of this skink. Most of the area preserve the typical autochthonous scrubs with Aleppo pines and only the lowlands show evidences of old plots, though nowadays are abandoned. Today, the biggest anthropic impact is the massive urbanization, such as estates and roads, in the southern half of Serra del Molar. New faunal surveys will help to clarify and more accurately assess the distribution of *C. ocellatus*, since it is a generalist species, cryptic and adaptable to the presence of humans and agriculture (Schneider, 1981; Schleich et al., 1996).

An alien population of *C. ocellatus* in the Iberian Peninsula raises a new management problem: the possibility of an ancient introduction in Serra del Molar, in addition to the semi-insular character of this area, could be arguments for its conservation. On the other hand, the possible competition with the native skink *Chalcides bedriagai* and the current connectivity with the surrounding regions, may raise arguments to control its population and even propose its eradication. Following the guidelines of the recent review about the status of allochthonous herpetofauna in Spain and management proposals (Santos et al., 2015), we believe it would be necessary to first carry out field surveys, with monitoring of individuals and experimental studies to assess the *C. ocellatus* interactions with the native biota, specifically the skink *C. bedriagai*, as well as to perform ecological niche models that might hint on the future distribution trends and possible expansion

of this species. The results of these proposed studies will help to evaluate the criteria in future management for *C. ocellatus* in Serra del Molar.

Finally, new efforts are needed in the herpetofaunal studies in archaeological contexts of the Iberian Mediterranean regions. The currently known data show that the first records of some Maghrebian species in the Iberian Peninsula are dated in recent chronology, during the Holocene (Bisbal-Chinesta and Blain, 2018). Paleo-Archaeoherpetology can help us to identify their arrival and the influences of the human factor on them.

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